THE LEEUWIN CURRENT:
an influence on the coastal climate and marine life of Western Australia

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Preface

This symposium was sponsored by the Royal Society of Western Australia, with additional support from the Western Australian Branch of the Australian Marine Sciences Association (AMSA). Its purpose was to bring together, for the first time, the multidisciplinary group of researchers studying various aspects of the Leeuwin Current. It is hoped that as a consequence of the symposium and this volume, further research into this unique and interesting current system will be stimulated.

It was appropriate that Dr George Cresswell should deliver the opening paper at the Symposium as his oceanographic researches during the 1970s led to the clear identification and naming of the Leeuwin Current. He can justly be termed the "father of the Leeuwin Current". It is equally fitting that Dr Joseph Gentilli, who presented the second paper, be the "grandfather of the Leeuwin Current", as he had shown the existence of tongues of warm water down the west Australian coastline a decade earlier.

All the papers in this volume were presented verbally at the symposium. Dr Bruce Hatcher's paper was read by Dr Bob Black. It is inevitable that there is a degree of overlap between some of the papers. We have tried to maintain a balance between minor repetition and the requirement for each paper to stand alone.

As we abhor the proliferation of "grey" (un-refereed) conference literature, all the papers in this volume have been refereed critically according to the normal standards of scientific publication. We are grateful to the following reviewers for their efforts to ensure that a high scientific standard has been maintained, and for their prompt cooperation:

Dr R Allan (CSIRO Division of Atmospheric Research)
Dr D Ayre (University of Wollongong)
Dr N Caputi (Western Australian Department of Fisheries)
Dr G Cresswell (CSIRO Division of Oceanography)
Dr C Crossland (CSIRO Institute of Natural Resources and Environment)
Dr S Godfrey (CSIRO Division of Oceanography)
Dr A Huyer (Oregon State University, USA)
Mr G Kendrick (The University of Western Australia)
Dr H Kirkman (CSIRO Division of Fisheries)
Prof A McComb (Murdoch University)
Dr J Middleton (University of New South Wales)
Dr C Pattiaratchi (The University of Western Australia)
Mr A Pearce (CSIRO Division of Oceanography)
Dr B Phillips (CSIRO Division of Fisheries)
Dr P Playford (Geological Survey of Western Australia)
Dr D Pollard (Fisheries Research Institute of New South Wales)
Dr G Poore (Museum of Victoria)
Dr D Saunders (CSIRO Division of Wildlife and Ecology)
Dr V Shannon (Sea Fisheries Research Institute, South Africa)
Dr J Stoddart (Kinhill Engineers)
Dr D Walker (The University of Western Australia)

The organising committee comprised the editors, and Nick D'Adamo, Peter Murphy, Lesley Thomas and Valerie Pearce. We thank CSIRO Floreat for allowing us to use their excellent conference facilities as a venue for the symposium, and all who assisted us on the day. The manuscript formatting was carried out at the Botany Department, and artwork was provided by the Centre for Water Research, both within The University of Western Australia. We record our appreciation of the contribution made by Ainsley Calladine with diagram transfers and advice on desktop publishing. We thank Fiona Webb for general assistance with word-processing.

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The Leeuwin Current - observations and recent models

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Abstract

The Leeuwin Current carries warm low salinity water from northwestern Australia into the prevailing equatorward wind to Cape Leeuwin and then across the Great Australian Bight. Current speeds to the west of the continent can exceed 0.5 ms^{-1}, while to the south they can exceed 1.5 ms^{-1}. In both regions the maximum speeds are encountered just beyond the continental shelf edge. Although the current is a low salinity feature to the west of the continent, once it rounds Cape Leeuwin it enters a regime of cold, low salinity waters so that it is then relatively high in salinity. The current frequently meanders and breaks out to sea forming both cyclonic and anticyclonic eddies. On its shoreward side it spreads across the continental shelf, commonly reaching the very near shore south of Western Australia. In this review a description of the Leeuwin Current is given by making use of observations ranging back to those of Flinders in 1803. Recent models of the current are found to be quite successful in describing many of its features.

Historical

If we define the Leeuwin Current (Church *et al.* 1989, Smith *et al.* 1991) as a stream of warm, low salinity water that flows at the surface from near NW Cape down to Cape Leeuwin and thence towards the Great Australian Bight (as suggested by the satellite image in Fig. 1), then we find evidence for it as early as the start of the last century. In May 1803 Flinders (1814) was set to the east between Cape Leeuwin and Albany at a little over one knot. Between Albany and the Recherche Archipelago (near Esperance) he reported the current to increase from the coast seaward. And "in coasting all around the Great Bight" he had no measurable current, suggesting, perhaps, that the current did not spread coastward across the wide continental shelf.

Along the west coast of Australia the earliest evidence for a current of tropical origin came from observations of warm waters and tropical marine flora and fauna around the Abrolhos Islands (~29°S) by naturalist Saville-Kent (1897). Also, early reports by fishermen described a southwards current between Geraldton and the Abrolhos Islands in winter which increased when northerly winds blew (Dakin 1919).

Halligan (1921) presented a chart of the currents around Australia (Fig. 2) and described how the warm comparatively light waters of the Indian Ocean would have to discharge to the south, since there is no northern outlet. With, as we will see, some precision, he described how a cold and heavy Southern Ocean current approached the south-west coast of Australia and dipped beneath the warm southerly drift. From the vicinity of Cape Leeuwin he reported "a warm southerly and easterly surface current" with speeds of 0.3 - 0.4 knots.

The August quarterly sea surface temperature map presented by Schott (1935) clearly showed warm waters (>16°C) to have been carried around Cape Leeuwin and eastward. This is reinforced by his winter (August-September) current chart (Fig. 3), which shows the Leeuwin Current more or less as we know it.

Southward flow of low salinity waters in autumn and winter and northward flow of high salinity waters in summer were seen from drift bottle measurements and hydrological observations by Rochford (1969).

Historical bathythermograph data were interpreted by Gentilli (1972) to show that the throughflow from the Pacific to the Indian Ocean in autumn and winter was isolated by a reversal of the flow in spring. This water then achieved thermal homogeneity over the summer to become a 'raft' of warm water, which spread southward during the following autumn and winter (Fig. 4). The 'raft' description was coined in the 1950's by Dr D L Serventy during discussions with fishermen who mentioned the warm water and the tropical species in it (Gentilli pers. comm. 1991).

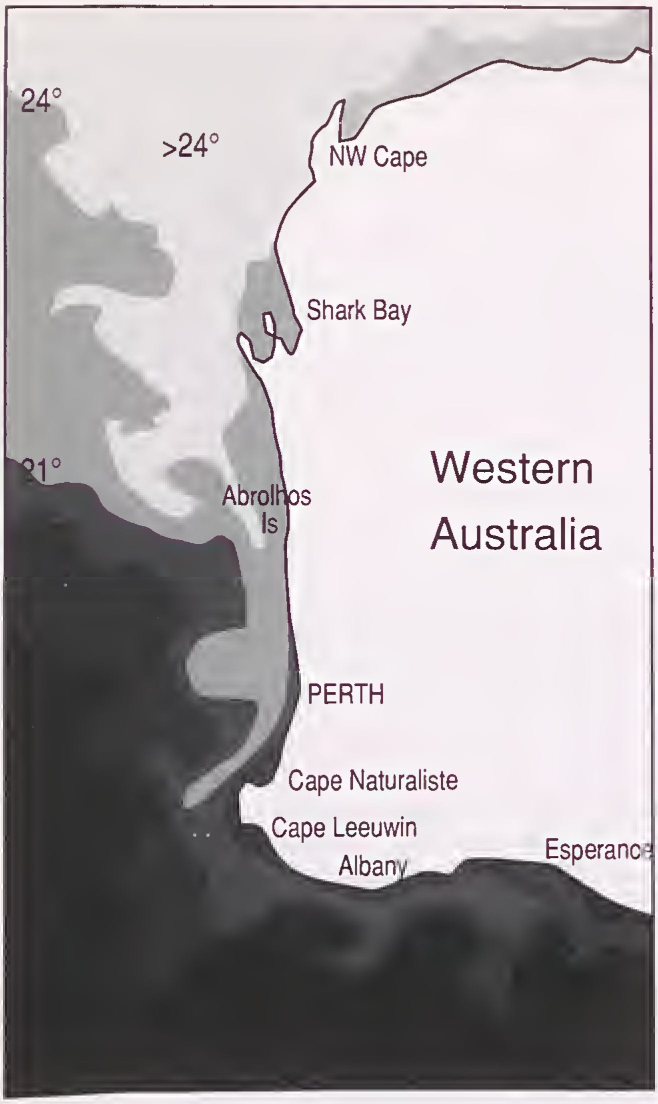


Figure 1 The temperature distribution off western Australia as determined from an infrared satellite image from 15 June 1984. The Leeuwin Current starts as a broad fan of warm water (>24°C) off the northwest and progresses southward to Cape Leeuwin and then eastward to the Great Australian Bight. There are eddies, meanders and offshoots associated with the Leeuwin Current. Mixing, radiation and evaporation change its water properties as it progresses.

Some fifteen years ago the response of satellite-tracked drifters (Cresswell & Golding 1980) to the flow of water of tropical origin was quite dramatic (Fig. 5), showing a drift to Cape Leeuwin and then eastward, as well as the interaction between this drift and the eddies offshore from it. Cresswell & Golding called the drift the Leeuwin Current, after the Leeuwin (Lioness in English), a Dutch ship that explored eastward towards the Bight in 1622.

The Leeuwin Current flows principally in autumn and winter. It is unusual in that it flows southward and into the wind. Other current systems on the eastern sides of oceans - the Benguela, Canary, Peru, and California current systems of the Atlantic and Pacific Oceans - flow equatorward. Further evidence for the Leeuwin Current from ship drift observations, research vessel surveys, and biological data sets is reviewed by Church *et al.* (1989) and Batteen & Rutherford (1990). In addition, analyses of the data from the Leeuwin Current Interdisciplinary Experiment (LUCIE) in 1986/87 are proceeding with some of the first findings being reported by Smith *et al.*(1991).

In the following sections we outline the features of the Leeuwin Current and the results of several conceptual and numerical models.

Features of the Leeuwin Current

Oceanic scale

It is instructive to take a large scale view of the salinity west of Australia in March along a line several hundred kilometres offshore running from Java to Antarctica (Fig. 6). Data collected by Deacon on RRS Discovery in 1936 and by Rochford on HMAS Gascoyne in 1963 have been combined - both were presented by Wyrtki (1971).

The section shows a number of interesting features:

- Near Java, there is low salinity water from river runoff and throughflow from the Pacific Ocean that tapers away to the south. Beneath the surface plume and down to the depth of the sill in the Timor Trench (about 1400m) are the near-constant salinity waters of the Banda Sea where they have had a residence time of some tens of years.
- Near Western Australia the excess of evaporation over precipitation produces dense salty South Indian Central Water that sinks and slowly moves northward.
- In the Southern Ocean, precipitation and ice melting result in a sinking plume of cold, fresh Antarctic Intermediate Water that also flows with a northward component .
- On the Antarctic continental shelf, where winter freezing excludes salt, there is a cold salty plume that sinks and moves northward as Antarctic Bottom Water. In summer, the surface water near Antarctica is warmed and it is diluted by ice melting. This produces the Antarctic Surface Water, which also moves northward.
- The southward-flowing Deep Water, which has its origins in the South Atlantic, replaces those northward flowing waters.

So then, where is the Leeuwin Current?

To see the current one must move closer to the continent - in autumn and winter when it flows strongest. The next diagram (Fig. 7) concentrates on the region from just north of NW Cape down to Cape Leeuwin - a voyage by HMAS Diamantina in August

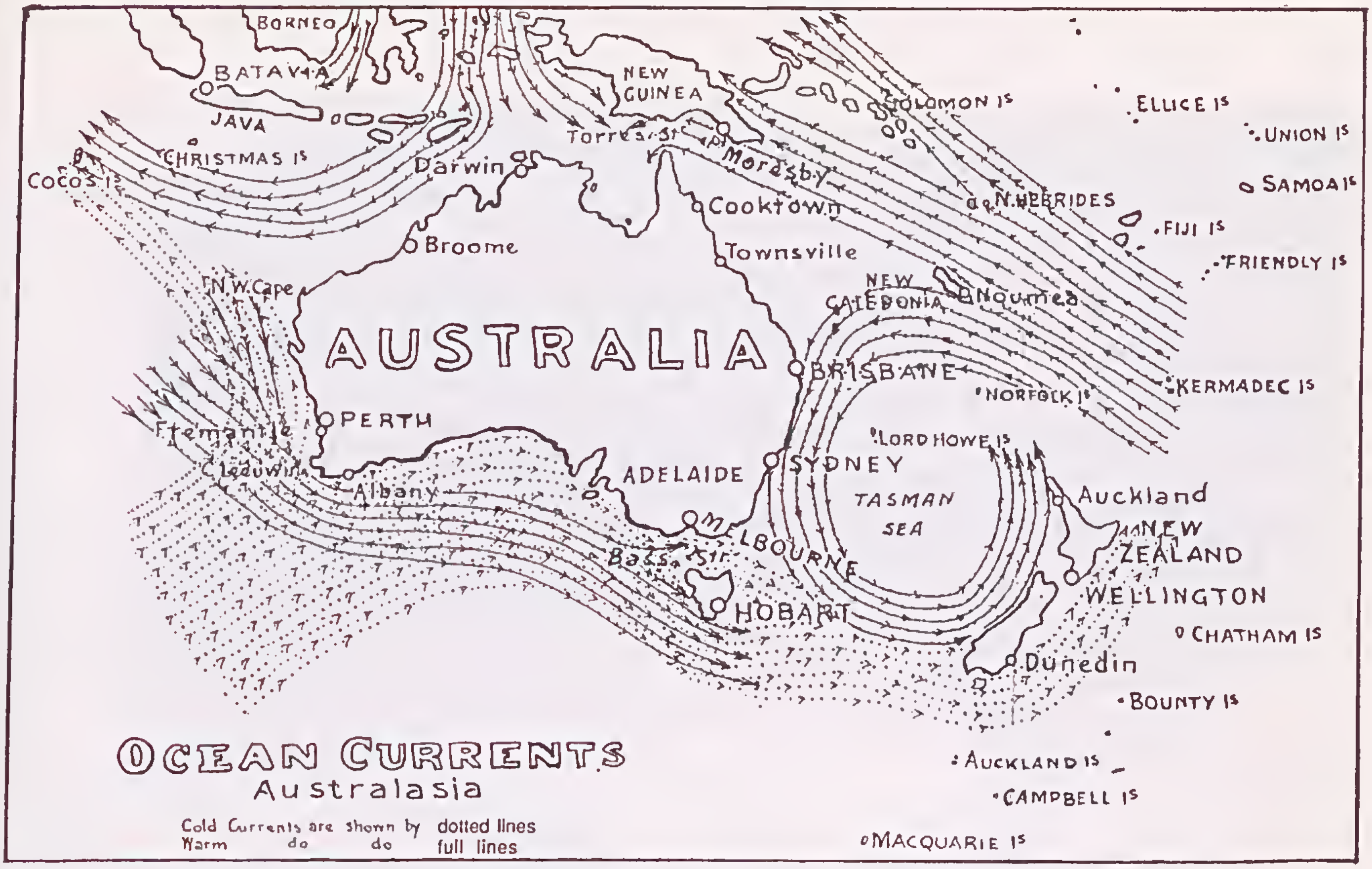


Figure 2 A current chart from Halligan (1921) showing a warm surface current flowing down the western Australian coast and a cold northward flowing current which sinks beneath it.

Figure 3 A current chart for the Australian region in winter (August-September) taken from a global chart by Schott (1935). The Leeuwin Current is readily apparent.

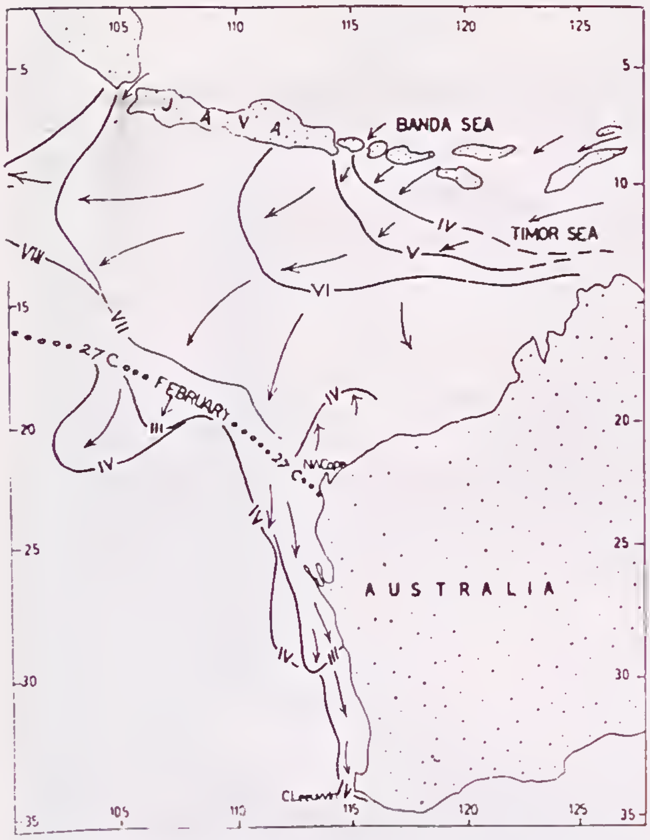


Figure 4 The position occupied by the 'raft' of warm water, originally from the throughflow, in February, followed by its progression to the south as the Leeuwin Current (from Gentilli 1972).

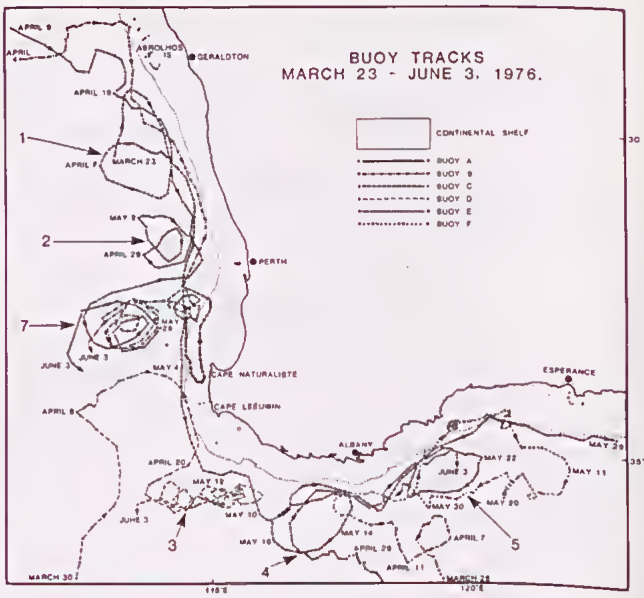


Figure 5 The tracks of the six drifters that were influenced by the Leeuwin Current or its associated cyclonic eddies (numbers 1-5) or the anticyclonic eddy (number 7) during the period March 23 to June 3, 1976 (from Cresswell & Golding 1980).

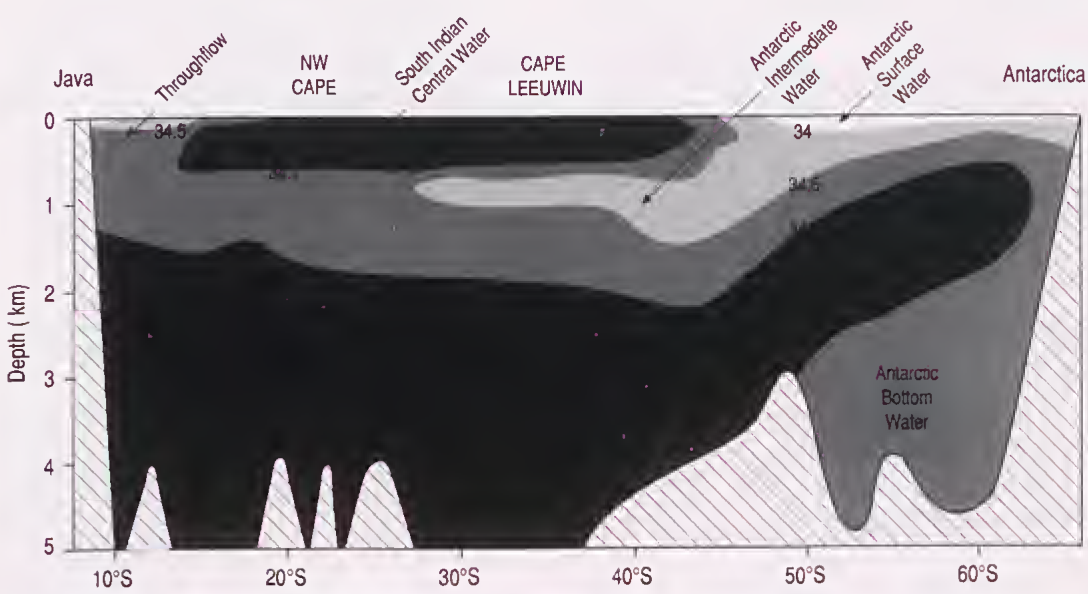


Figure 6 A salinity section looking towards Australia from several hundred kilometres offshore between Java and Antarctica. The data were collected by RRS Discovery in 1936 and HMAS Gascoyne in 1963 and presented by Wyrtki (1971). They were composited for this diagram.

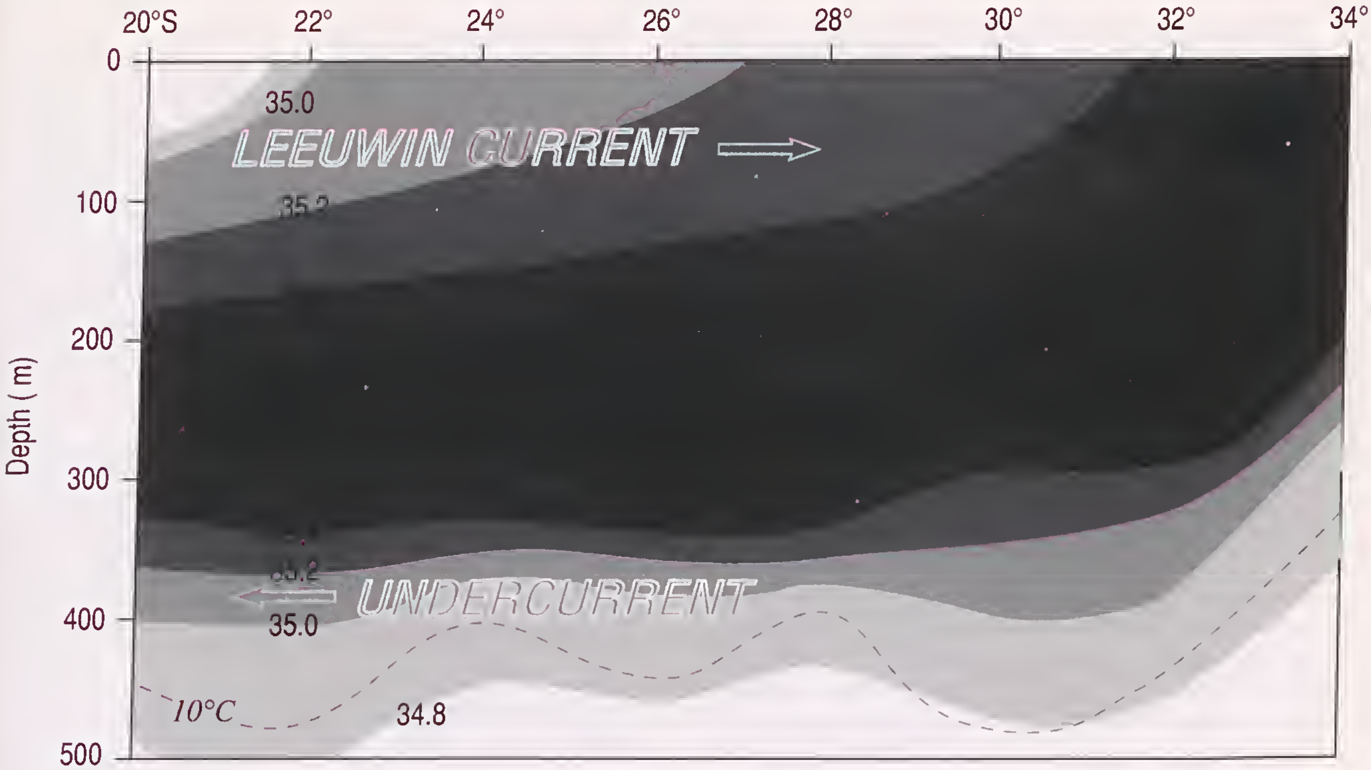


Figure 7 The salinity structure at the shelfedge and down the continental slope from NW Cape to Cape Leeuwin showing the low salinity Leeuwin Current and the Undercurrent, which carries South Indian Central Water and Subtropical Oxygen Maximum waters northward (from a cruise by HMAS Diamantina in August, 1971).

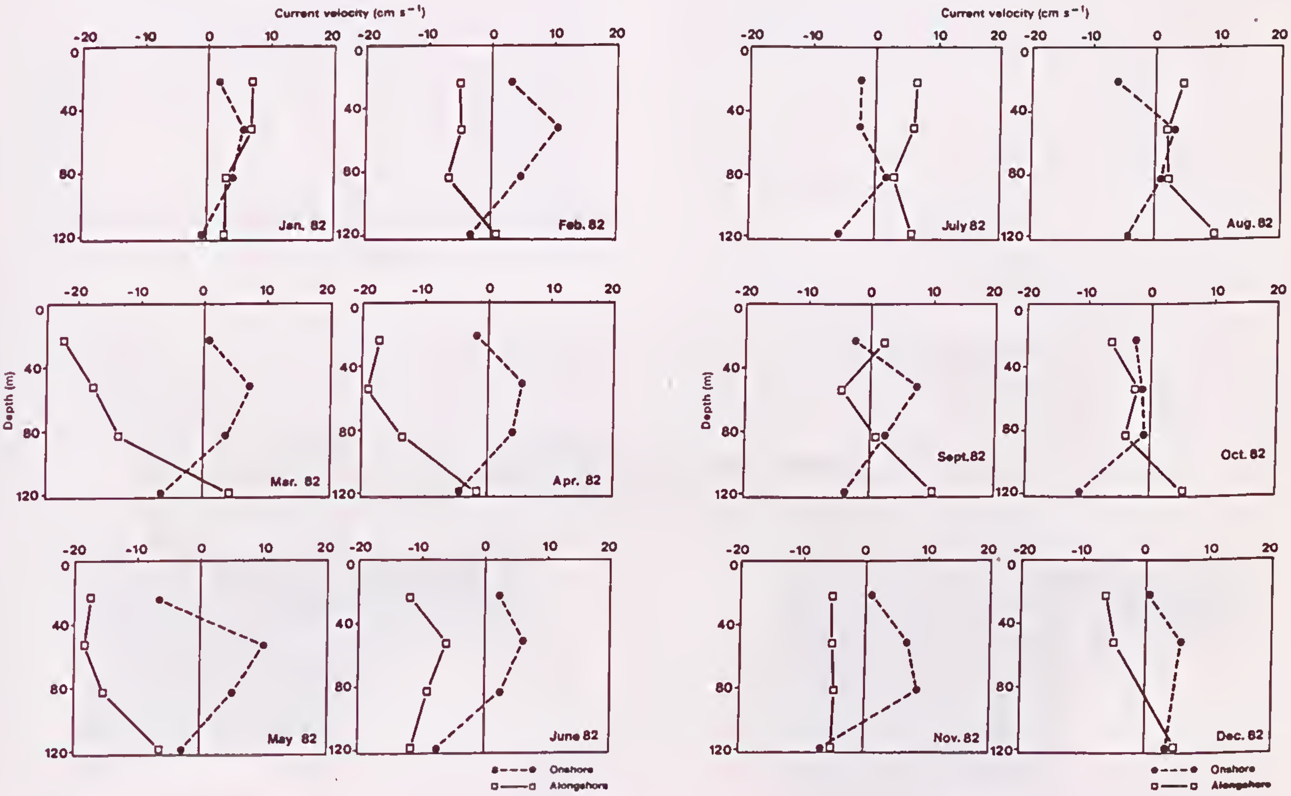


Figure 8 Vertical profiles of monthly average onshore and longshore currents measured at North Rankin (19° 35'S, 116° 05'E; water depth 123 m) on the southern NW Shelf in 1982. Negative alongshore currents represent southward flow and hence contribute to the Leeuwin Current (from Holloway & Nye 1985).

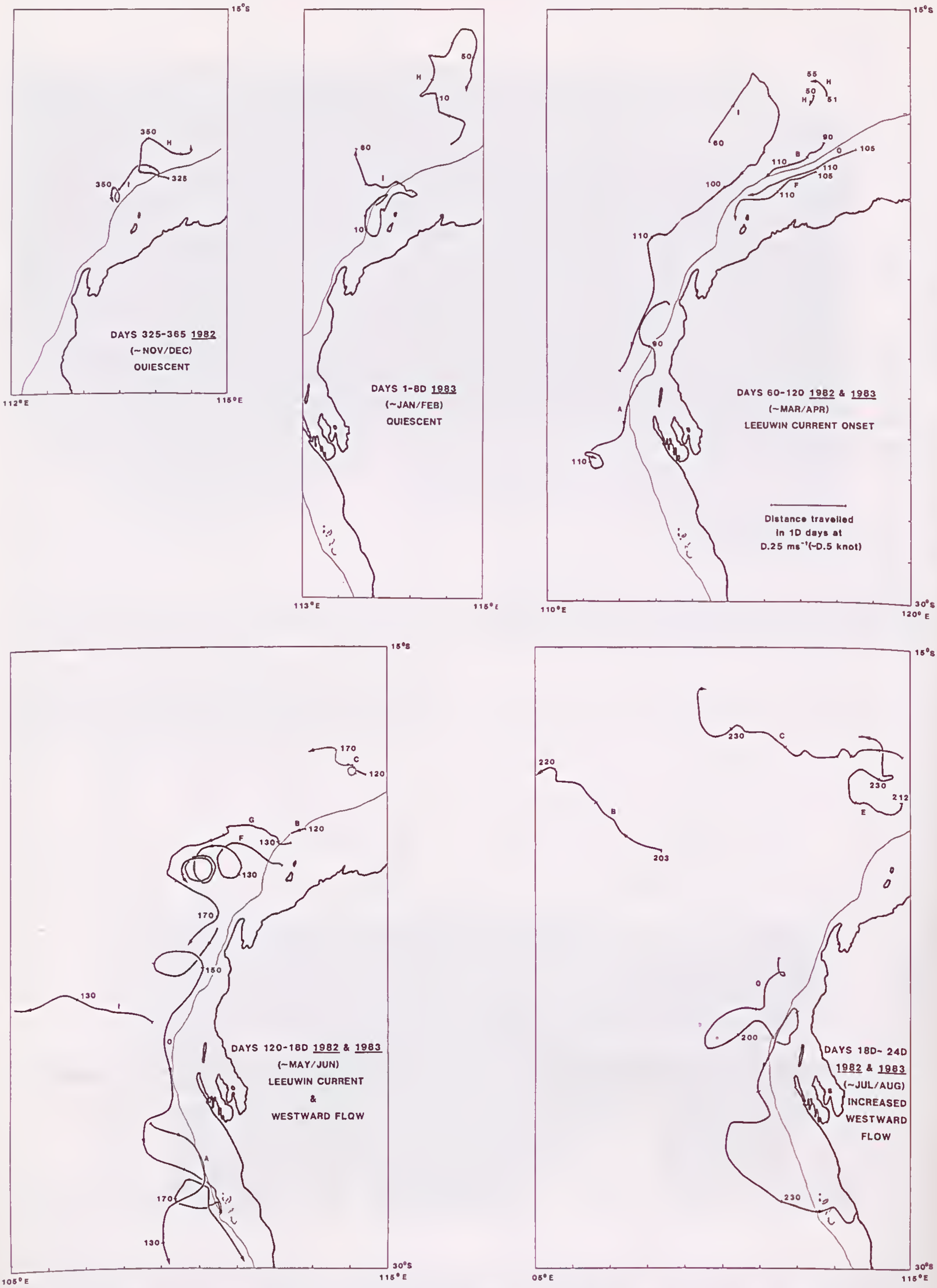


Figure 9 Satellite tracked drifters near and offshore from the Holloway and Nye (1985) moorings in 1982 and 1983 (see Figure 8).

1971. The diagram shows the salinity structure at the shelf edge and down the continental slope. The Leeuwin Current is the low salinity, warm wedge that extends southward to 30°S. Beneath it is the undercurrent sliding northward carrying high salinity South Indian Central Water as well as oxygen rich waters (not shown in this diagram). As the Leeuwin Current progresses southward it cools and becomes saltier because of evaporation and mixing with the South Indian Central Water.

Source

What is it that takes place at and south of the source area off NW Australia in autumn?

Current meter data for 1982/83 (Fig. 8) revealed a contribution to the Leeuwin Current by NW Shelf waters (Holloway & Nye 1985). It was strongest from February to June reaching 0.2 ms^{-1} in March-April-May in 1982.

Satellite tracked drifters near and offshore from the moorings in 1982 and 83 (Fig. 9) revealed an interesting seasonal behaviour:

> From November to late March the situation could best be described as quiescent, with the drifters moving slowly (~0.1 ms^{-1}) and following no consistent path.
>
> At the start of April, however, there was a dramatic move poleward at speeds of about 0.2 ms^{-1} on the shelf and up to 0.3 ms^{-1} off the shelf. A drifter that rounded NW Cape in late April accelerated to 0.5 ms^{-1}.
>
> May through August saw predominantly poleward flow with an increasing tendency for the region to feed the South Equatorial Current.

West coast

Off NW Cape the warm low salinity source of the Leeuwin Current is broad and shallow (400 km by 50 m), but in running southward it tapers to less than 100 km and deepens to more than 100 m, while having speeds that can exceed 1 knot. The warm low salinity waters carried by the Current (Fig. 10) are commonly encountered just beyond the continental shelf edge, but they can spread half way to the coast, except in summer when a wind-driven high salinity northward flow occupies most of the shelf. Incidentally, in summer there is a region of strong shear on the outer shelf between the northgoing shelf waters and the southgoing waters further out to sea (Cresswell & Golding 1980 - their Fig. 7).

A number of current meters moored mid-shelf off Dongara and Rottnest Island (near Perth) in the mid 70s (Fig. 11) indicate the influence of the Leeuwin Current flowing southward at ~0.2 ms^{-1} (Cresswell *et al.* 1989). At all times of the year the mid-shelf currents were strongly influenced by passing weather patterns (Fig. 12), which resulted in current variations of up to 0.5 ms^{-1} and sea level changes of about 30 cm. In summer, atmospheric troughs from the north interrupted the northward wind stress and allowed the shelf waters to move south. In winter, the passage of lows near and south of Cape Leeuwin gave rise to strong northwesterly winds that augmented the southward Leeuwin Current flow on the shelf.

South coast

The Current appears to take on a new character once it rounds Cape Leeuwin. It enters a regime where its salinity is higher than ambient, rather than the reverse as is the case west of the continent where it flows through high salinity South Indian Central Water. In the second (fresher) regime the Leeuwin Current has been observed to carry with it a sheath of salty South Indian Central Water. The sheath is then slowly lost downstream through energetic mixing with the fresher offshore waters (Cresswell & Peterson unpubl.).

It is just beyond the shelfedge between Cape Leeuwin and the Bight that the Leeuwin Current reaches its greatest speeds of more than 3 knots, or 1.5 ms^{-1} (Fig. 13). It is quite narrow, a band less than 20 km wide contains the speeds exceeding 1 knot (0.5 ms^{-1}). Across the shelf the currents range down from 0.5 ms^{-1}. The offshore edge is marked by a temperature front of several degrees Celsius.

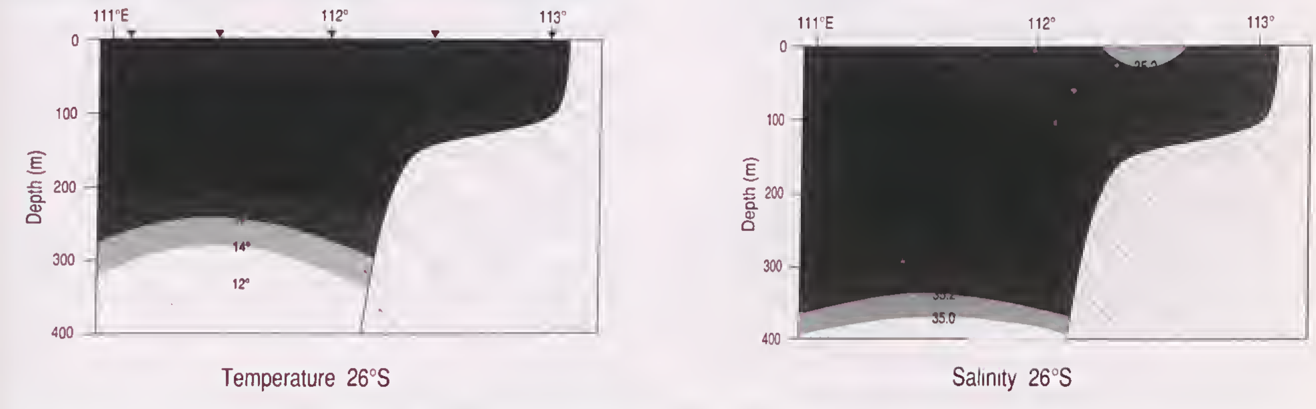


Figure 10 A section at 26°S made by HMAS Diamantina in August 1971 showing a) temperature and b) salinity.

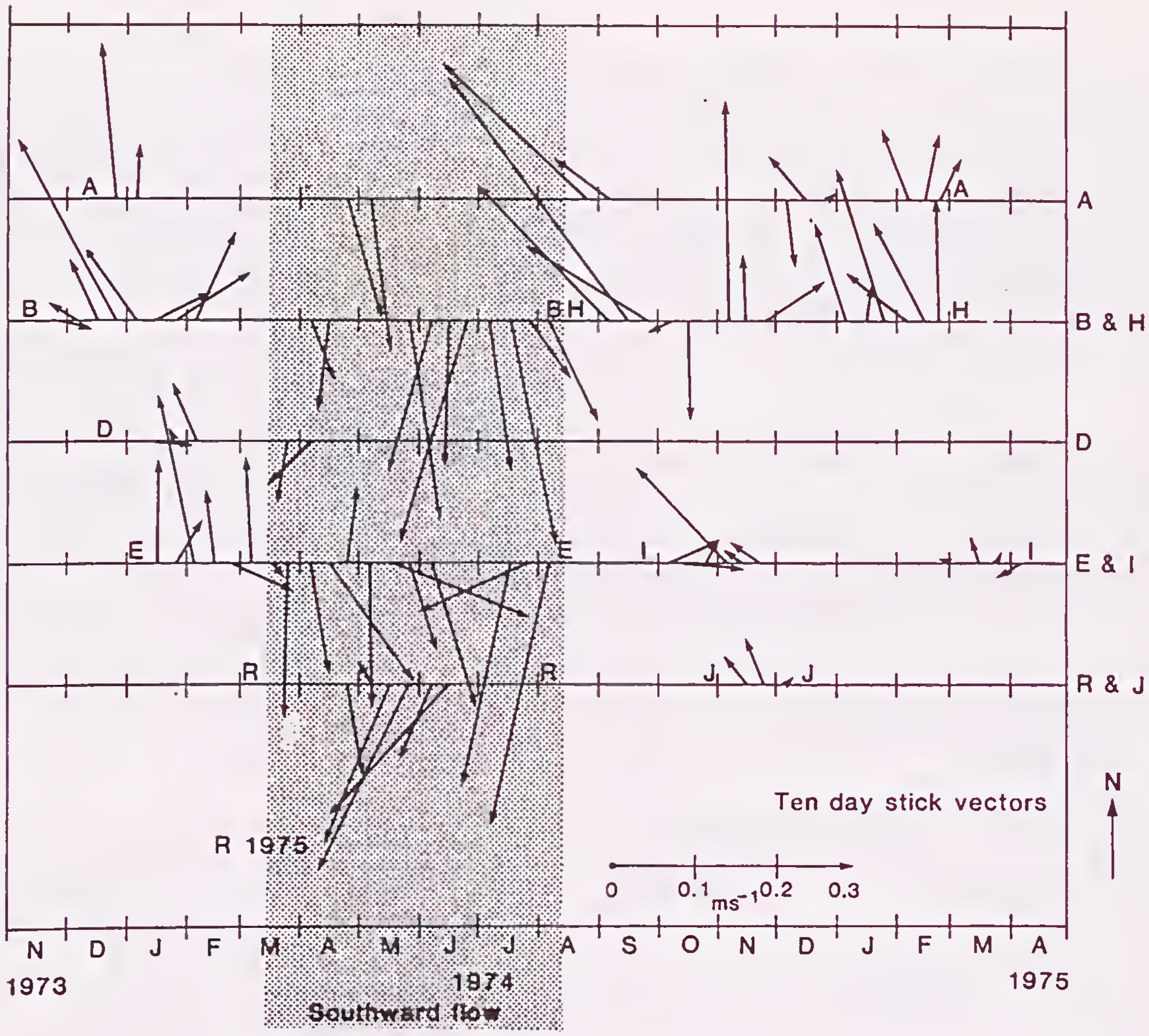


Figure 11 Current meter measurements from mid-shelf sites near the Abrolhos Islands (except for R which was near Rottnest Island off Perth) arranged according to site and time. The stick vectors are ten-day averages. The stippled period, from March to August, shows the period of strongest southward flow, probably the result of the Leeuwin Current spreading onto the shelf (from Cresswell *et al.* 1989).

There are places where the current breaks out to sea (Cresswell & Golding 1980, Griffiths & Pearce 1985) and in June 1987 it was found that one of the offshoots had a trough-shaped cross section 50 km wide by 150 m deep with southgoing flow on the western side and northgoing flow on the eastern side (Cresswell & Peterson unpubl.). Many features of the offshoots have been reproduced in rotating laboratory tanks (Condie & Ivey 1988).

Some attempts to explain the current

Thompson (1984, 1987) concluded that the Leeuwin Current is driven into the prevailing wind by a longshore sea-level gradient and further that the wind forcing effects are diminished by deep mixed layers. In other words, the force of the northward wind is distributed over considerable depth and is therefore less effective in retarding the southward flow.

Godfrey & Ridgway (1985) examined the annual cycles of sea level and wind stress (Fig. 14). The annual average sea level shows a southward flow component near the coast, as indicated by the orientation of the sea level contours, which increases in strength southward from NW Cape. The annual average wind stress is strongly northward between Cape Leeuwin and NW Cape. (Further north, the wind has a strong component to the west and this may explain why drifters in the near-surface layer moved off in that direction to join the South Equatorial Current.)

However, the wind stress eases between March and October to reinforce the effects of the peak in sea level difference at the shelf edge between NW Cape and Cape Leeuwin from February to August (Fig. 15). Incidentally, during LUCIE in 1986/87 the seasonal variation in the strength of the Leeuwin Current seemed to be the result of variations in the wind stress and not in the alongshore pressure gradient, which had little seasonal dependence (Smith *et al.* 1991).

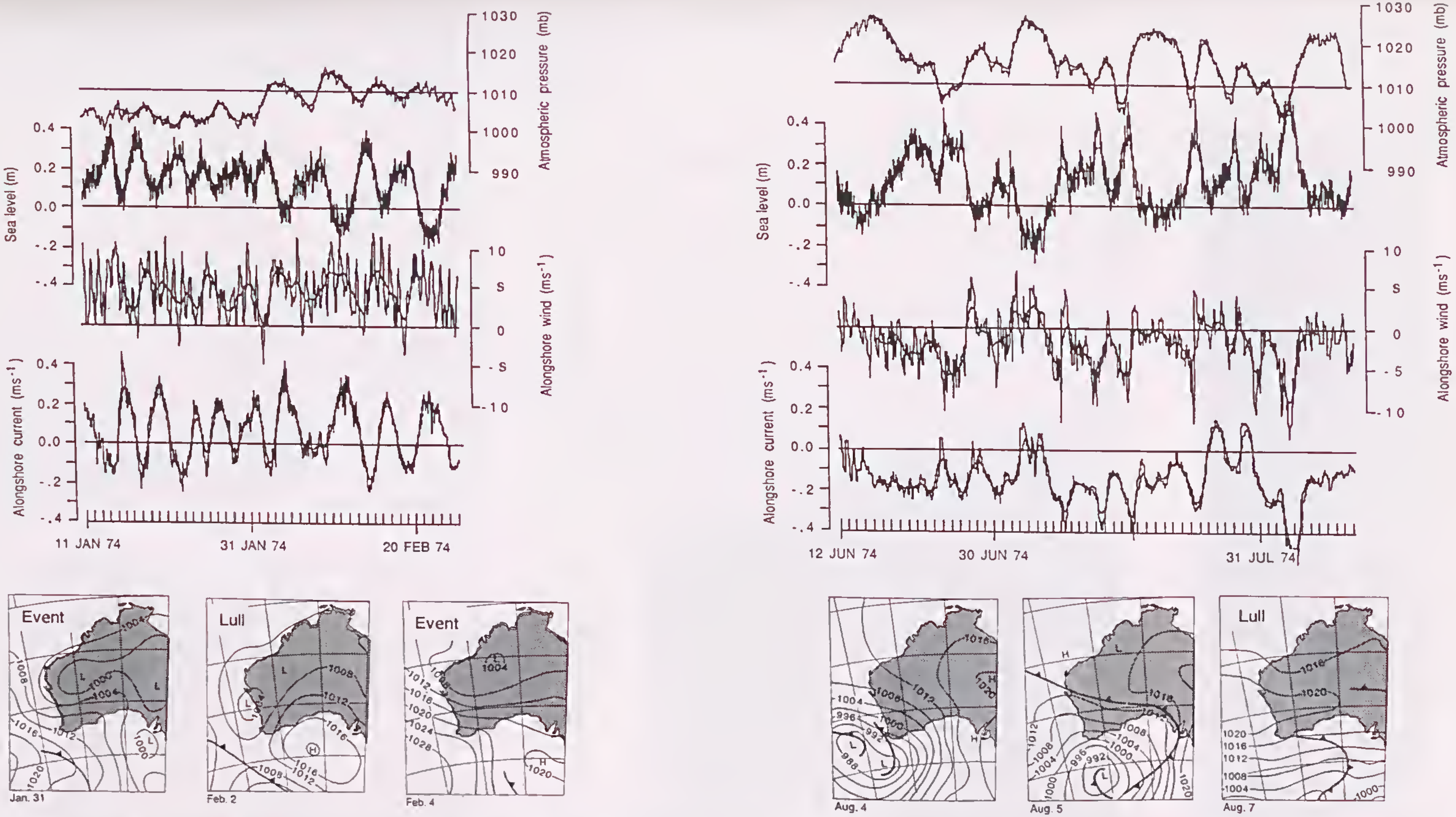


Figure 12 Time series of smoothed and unsmoothed atmospheric pressure, sea level (tides removed) and alongshore wind from Geraldton and the current 10 m above the bottom at a site near the Abrolhos Islands where the depth was 42 m in summer and 46m in winter (from Cresswell *et al.* 1989).

a) Summer (January/February). (Upper panel) The strong sea breeze has little effect on the currents at the depth of the current meter. However, when the winds are northward (positive) for several days the sealevel falls and the currents are northward. Low wind speeds produce elevated sea level and southward currents. (Lower panel) An example showing the synoptic atmospheric pressure charts for a period of low winds (Feb 2) that allows southward flow on the continental shelf. Before and after the winds have a southerly component that drives the flow northward.

b) Winter (June/August). (Upper panel) The current is predominantly southward due to the influence of the Leeuwin Current spreading onto the shelf. Winds with a strong southward component increase the current to almost 0.5 ms^{-1} and raise sea level by as much as 0.4 m. (Lower panel) An example of the synoptic atmospheric pressure charts at a time of enhanced southward flow on August 4/5.

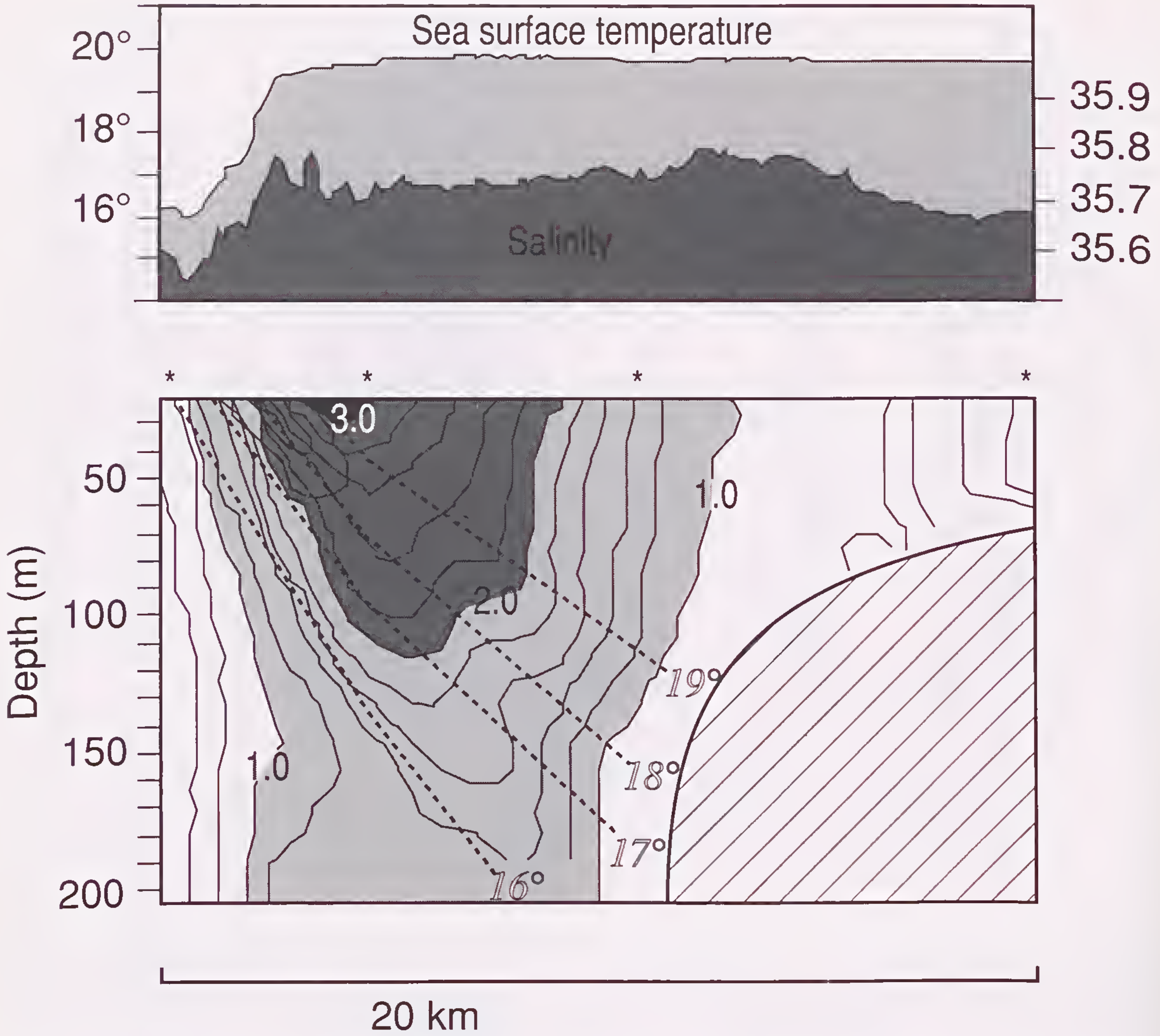


Figure 13 A section (bottom panel) showing the current structure measured by RV Franklin along a line out from the coast west of Albany in June 1987. Current speeds greater than 1.0, 2.0 and 3.0 knots have progressively darker shading. The isotherms measured by expendable temperature probes are shown. Note the surface temperature and salinity front (top panel) on the offshore edge of the Leeuwin Current where the speed dramatically decreases and where considerable overturn and mixing take place.

Weaver & Middleton (1989) used the Bryan-Cox General Ocean Circulation Model with seven vertical levels and initial conditions of a latitudinal variation of temperature and salinity. In addition, taking a lead from Gentilli's (1972) suggestion of a raft of warm water off NW Australia, they took all the water in the triangle east and north of NW Cape to have warm, less saline NW Shelf waters (28.3°C and 34.3ppt at the surface). They also allowed for a shelf that tapered from north to south along the WA coast. After running for 30 days, their model (Fig. 16) reproduced both the Leeuwin Current and the Undercurrent quite well -even to the extent of rounding Cape Leeuwin and flowing to the east.

Batteen & Rutherford (1990) developed a ten-layer model of the ocean between NW Cape and Cape Leeuwin using a climatological mean density and (in an alternative approach) included an input of water from the NW Shelf. In the latter case, as time passed the nature of the ocean temperature and sea level evolved from their initial setup in response to earth's rotation, eddy viscosity and bottom stress. After a time step of only ten days a Leeuwin Current had been established (Fig. 17). After much longer, an anticyclonic eddy formed off Perth, while north of it was a weaker cyclonic eddy. Both are reminiscent of the features revealed by the drifter tracks and ship data (Andrews 1977, Cresswell 1977).

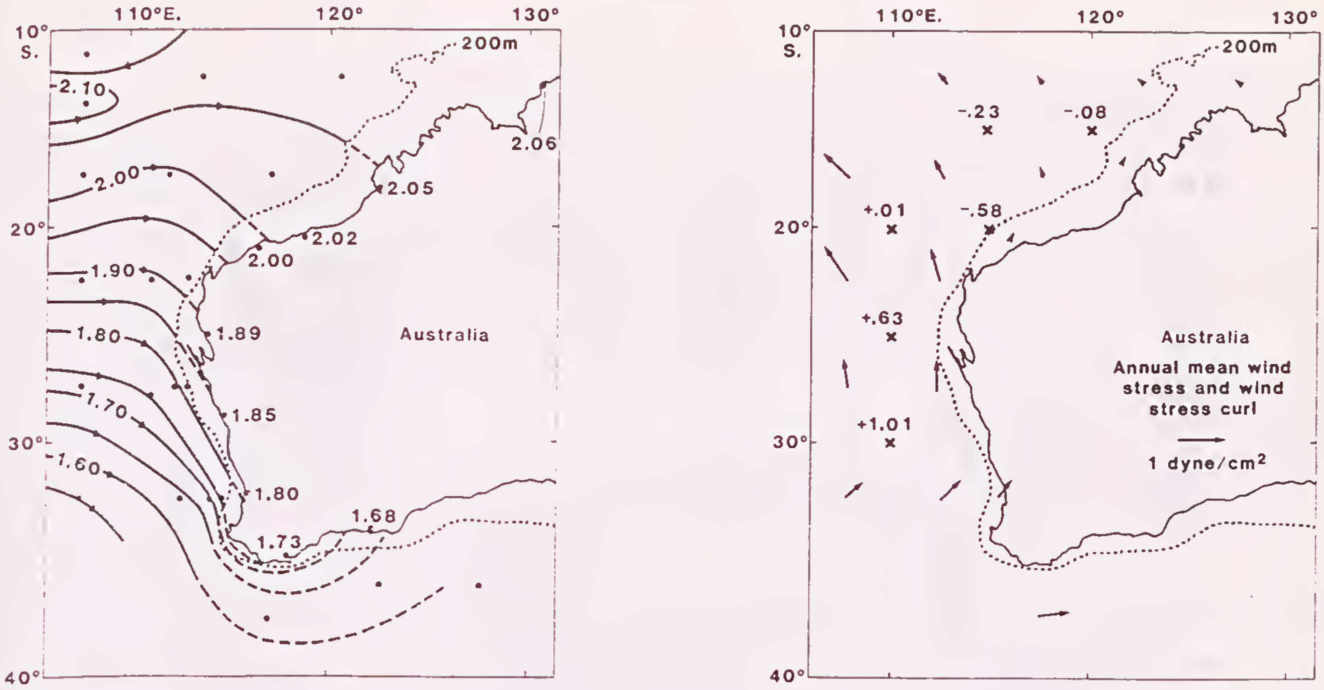


Figure 14 a) Contours of annual average steric sea level relative to 1300 db. The numbers along the coast give mean sea level at tide gauge locations. b) Annual average wind stress and wind stress curl (from Godfrey & Ridgway 1985).

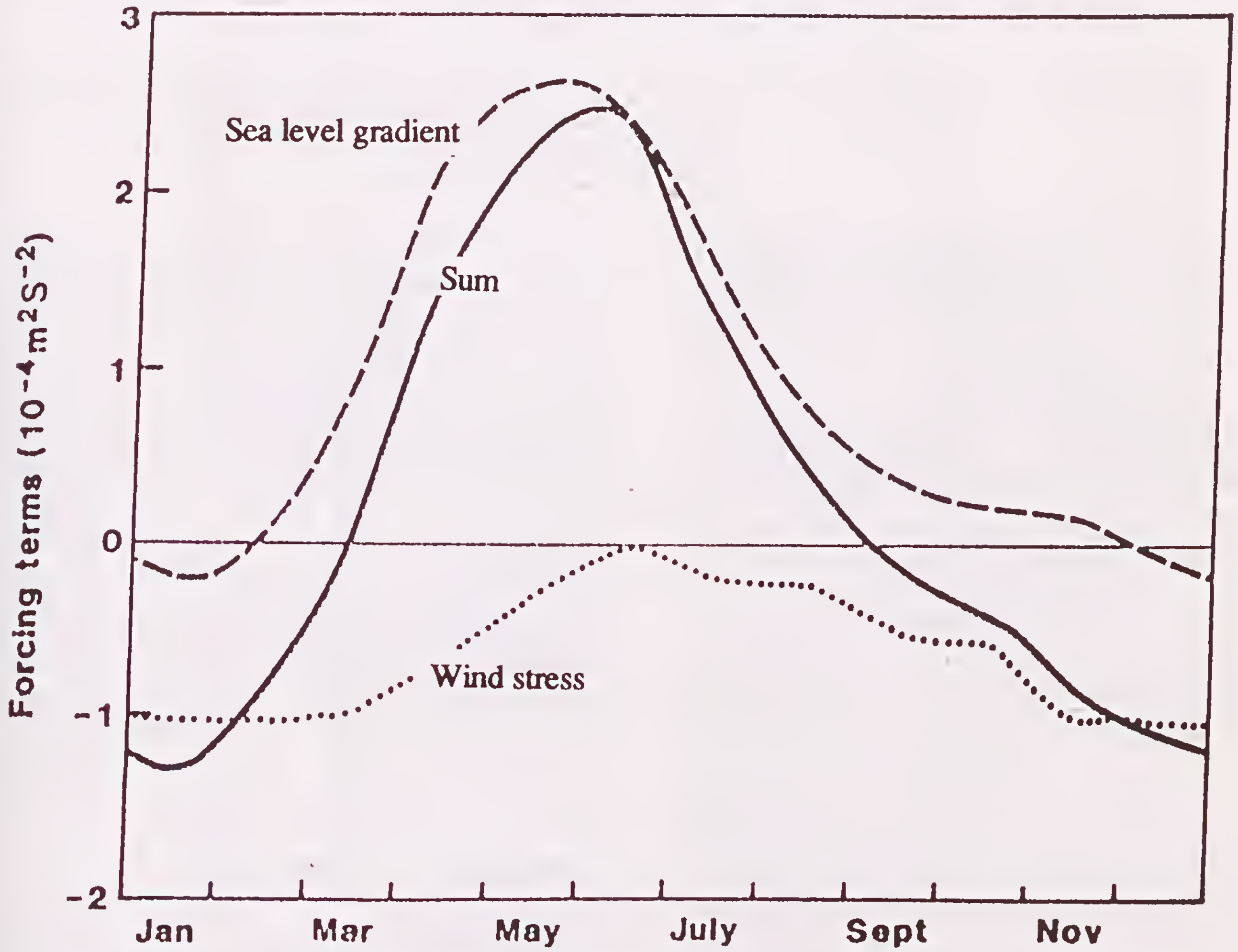
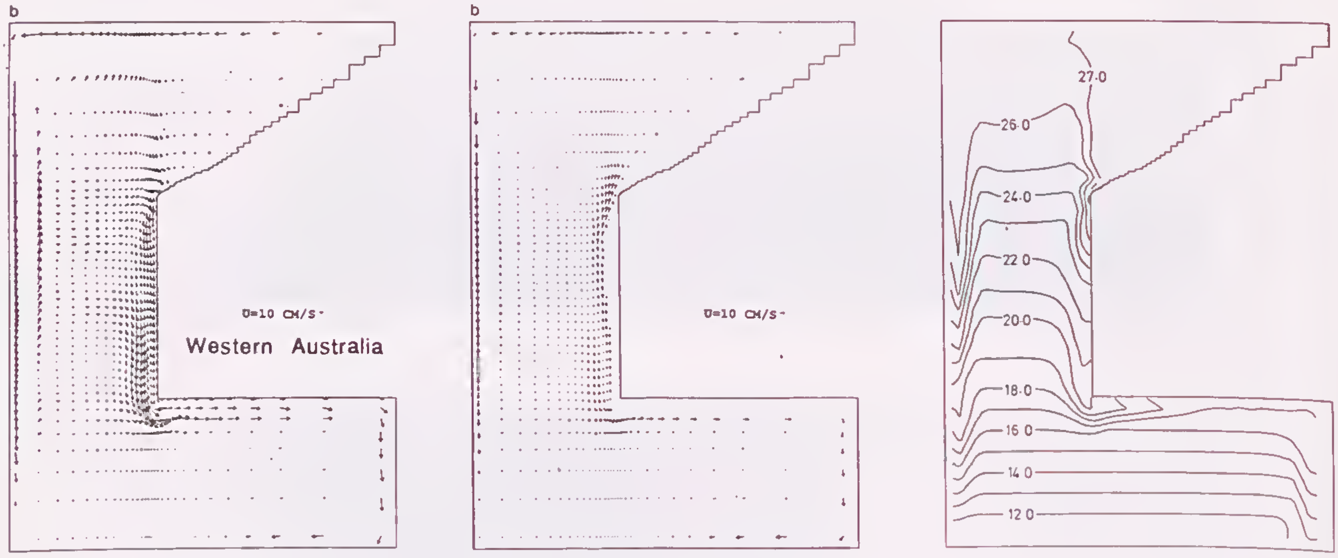


Figure 15 The annual cycle of the sum of the forces which drive and retard the Leeuwin Current (full line). These are the sea level gradient (dashed line) and the wind stress (dotted line) (from Godfrey & Ridgway 1985).



Surface current after 30 days | 350 m current after 30 days | Surface temperature after 30 days

Figure 16 The output from the model of Weaver & Middleton (1989) after it had run for 30 days. The Leeuwin Current can be seen rounding Cape Leeuwin in the representation of both the surface current (left panel) and surface temperature (right panel). The undercurrent can be seen at 350 m (middle panel).

Surface temperature and current

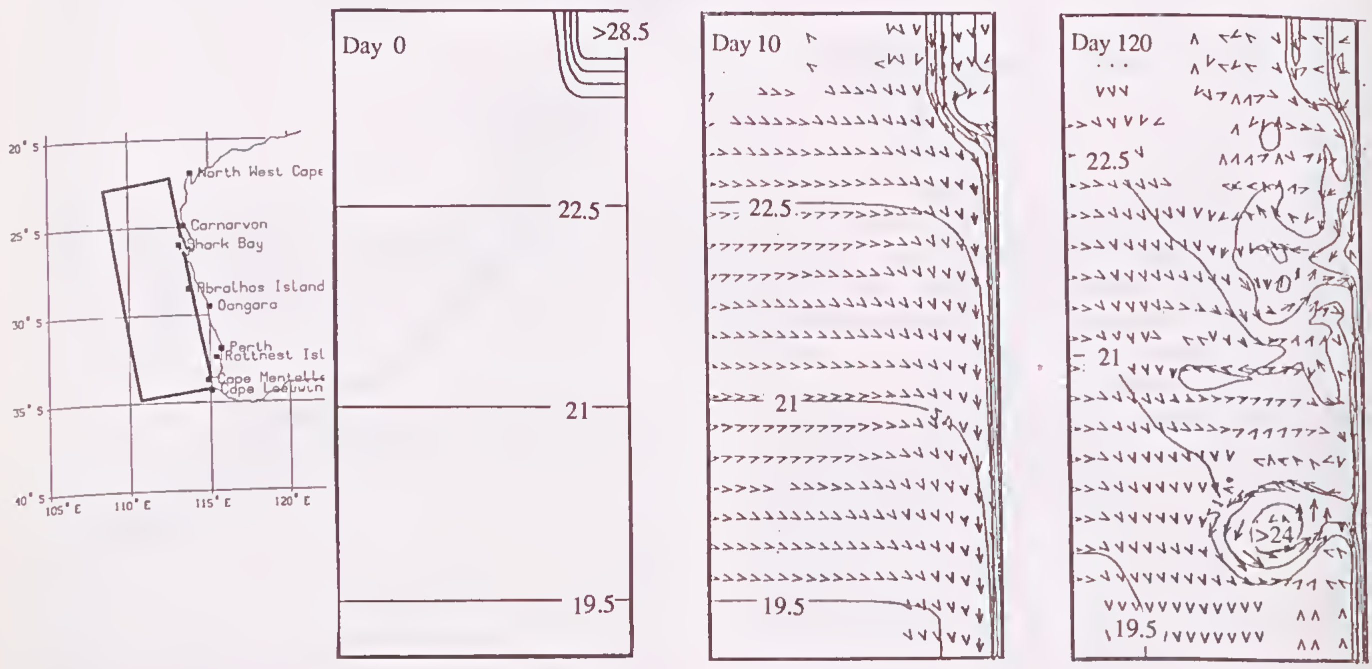


Figure 17a The initial conditions and selected results, at days 10 and 120, for surface temperature and surface currents from the model of Batteen & Rutherford (1990). The current speeds in the anticyclonic eddy off Perth are about 0.5 ms^{-1}.

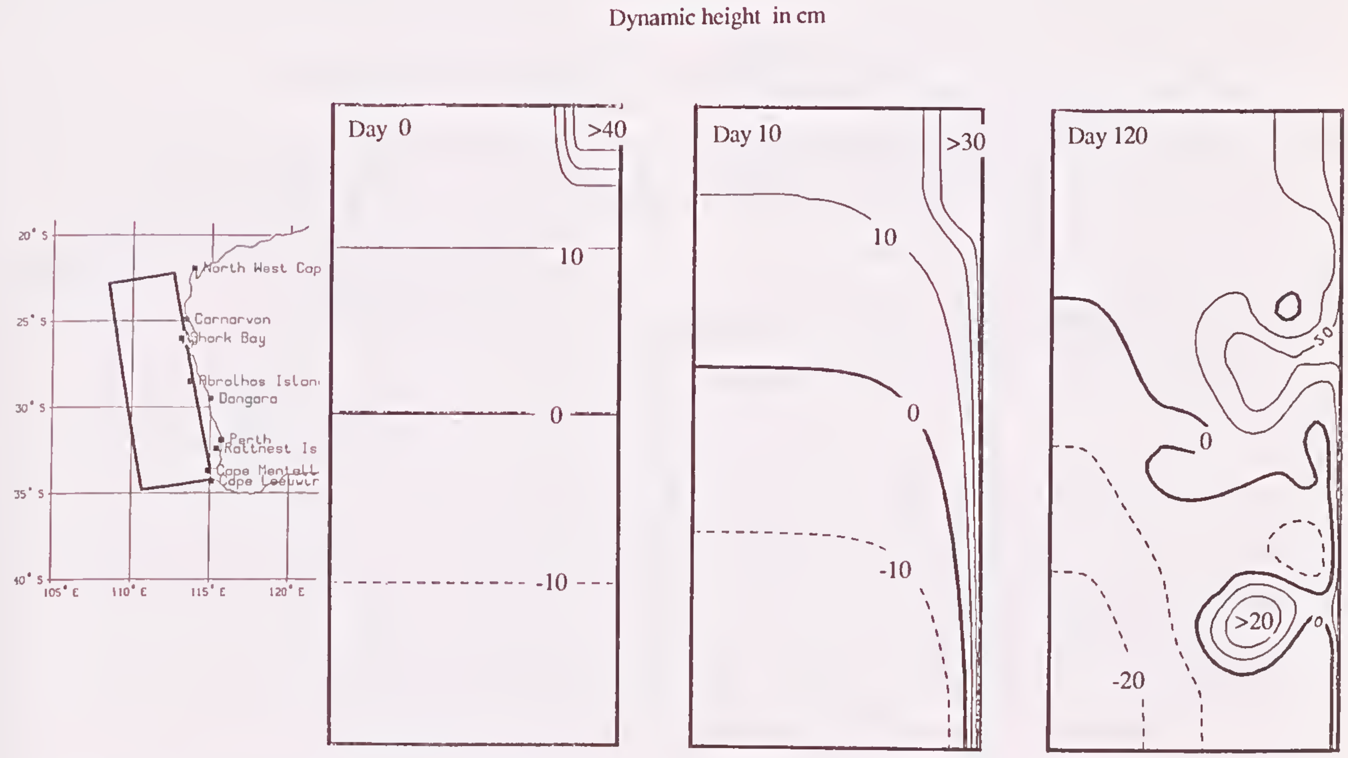


Figure 17b The initial conditions and selected results, at days 10 and 120, for dynamic height from the model of Batteen & Rutherford (1990). The current speeds in the anticyclonic eddy off Perth are about 0.5 ms^{-1}.

Concluding comments

Models now reproduce many of the features of the Leeuwin Current, such as rounding Cape Leeuwin, having an undercurrent and generating eddies. However, the challenge of developing a model which will produce the annual and interannual variations of the Leeuwin Current remains. Also, such a model will ideally need to mesh in with models of continental shelf circulation.

The immediate future will see the launching of satellites such as ERS-1 and TOPEX/POSEIDON which are capable of measuring sea surface elevation, roughness and winds. This information will be used along with ship, drifter and tidal data to constantly update models, rather than have them rely on climatological means.

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Homologous peri-oceanic west coast climates in the southern hemisphere

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Abstract

Comparisons and analyses of similarities and differences between these climates in the three southern continents have revealed further aspects of the uniqueness of the Western Australian peri-oceanic and coastal climate.

In 1934 Meinardus published his rainfall map of the world, which clearly showed that the driest areas above the oceans were slanted SE-NW between 20° and 10° S off South America and Africa; at their origin, they encroached over the continental shores. The climatically corresponding area off Australia was (a) further south, between latitudes 25° and 20°S, (b) not slanted, (c) slightly offshore, clearly away from the coast, and (d) much smaller. In winter, low cloud, steady rain and passing showers about 30°S are frequent on the Western Australian coast and practically absent from the western coasts of Namibia and Chile (McDonald 1938). The annual rainfall off the west coast at 32°S is nearly 750 mm in Western Australia, under 300 off Chile and under 200 off Namibia. Near 24°S it decreases to under 200 mm off Western Australia, nearly nil off Chile and perhaps 25 mm off Namibia (Gentilli 1952a).

Biel (1929) had already shown that rainfall also varied to a different extent and over very different areas in the three southern continents, the Australian region of high variability being the smallest and more clearly restricted in latitude, whereas the South American area of high variability had great meridional extension and came fairly close to the Equator.

Ship observations collated by McDonald (1938) recorded about the same prevalence of southerly winds along the western subtropical coasts of the three continents, but their force was greatest near Western Australia and lowest near Chile, where calms were most frequent. Haze was more frequent near the African coast.

World maps of surface air temperatures for January and July (*eg* in Blüthgen 1966 or Newton 1972) and for each month (NOAA 1984 ff.) show equatorward bending of isotherms along the western coasts of all continents except Australia.

Atlases and books contain small rainfall maps, but in general the class intervals between isohyets do not allow adequate intercontinental comparisons. It was well known that dry climates continued equatorwards in South America and Africa, but since the Western Australian coast slants north-eastwards and eventually eastwards (Cape Londonderry, its northernmost point, is at 14°S) the pursuit of these and similar comparisons just did not eventuate.

Progress in meteorological observations and recordings has made it possible to analyse more climatic data in more sophisticated ways, thus isolating additional significant climatic information. Dynamic climatology, particularly with regard to the frequency, morphology and behaviour of tropical cyclones and the subtropical jet stream, has added to the knowledge and understanding of climatic differences between these homologous coastlines. The relevant factors and events may also originate at great distance, as is the case with El Niño, but are nevertheless very significant - their significance being subject to a considerable time lag.

A detailed comparison of the climates of the southern continents' western coasts shows differences which can be traced back to latitudinal extent and vertical configuration. Upper air analysis shows promise and some evidence of meaningful relationships as well as significant regional differences.

Most important regional climatic differences however are due to ocean water circulation and particularly differential surface temperatures.

Introduction

The term *homologous* defines the latitudinal limits of this study: west coasts occur in all three continents in the Southern Hemisphere, but the Western Australian coast has the shortest span of latitude (only between 14 and 35°S) and is therefore the maximum common factor. Africa and South America continue further north towards the equator, and South America continues further south into the higher latitudes. The term *peri-oceanic* has been added in order to include the climate of the air above the coastal waters, distinct from the climate of coastal and interior localities and more closely associated with ocean surface temperatures. Such concepts are illustrated by Fig. 1, which appears after the historical section. The position of the three regions on the globe places each one of them under the influence of the eastern margin of the quasi-stationary anticyclone which dominates the ocean offshore (Alissov 1954), but the degree of this influence is already a valid differential criterion, with western South America rigidly controlled by the Andean barrier, southwestern Africa occasionally swept by continental influences, and Western Australia being more continental than oceanic alternately in the north and in the south at the opposite seasons of the year. Such differences are shown, for instance, in Fig. 6.

Early observations: Western Australia

Early, isolated observations of these climates did not allow any comparative analysis, but on the other hand were not hidebound by official rules and allowed more scope for keen individual observers. Captain King (1827) made careful weather observations along the Western Australian coast between 1818 and 1822. In 1827 Captain Stirling observed "that the sea-breeze on this coast is usually at S.S.W., and is therefore charged with moisture and very cool; this moderates the action of the sun in summer... It is also remarkable that the [early morning]* land wind blowing from these mountains [presumed higher and snow-capped further inland!] is a cold wind... and from the alternate operation of these two winds, which seldom leave an intervening calm, the air, notwithstanding the sun's great heat, is cool and agreeable, except in spots which are sheltered from the breeze, or during calms" (in Cooke 1905). Some of the earliest climatic observations at Perth, published by Irwin in 1835, were quoted by Mühry (1862): "there are two seasons, the *wet* and the *dry*; the former, winter-like, lasts from March until November, with heavy rains only in August and September [should be June and July!]; the height of the rainless summer time is in January... Abundant dew is seen every night." Mühry adds that "the rains must come with northwesterly winds... Summer dew [at times!] condenses notwithstanding the continental easterlies because of the proximity of the sea as a source of moisture and the nocturnal cooling under a clear sky." Of 838 mm annual rainfall at Fremantle, 482 come in the three winter months (279 in July alone) and only 38 in the three summer months.

Cooke (1901, 1905) pointed out that the winter "sets in, as a rule, rather abruptly" and gave the dates of the first heavy winter rains at Perth from 1880 to 1905. "Owing to this tendency for the rain to fall principally in heavy showers and at night... the general impression of the Perth winter is that of a succession of fine, bright, calm days, varied occasionally by a severe but brief storm. The weather is, on the whole, delightful, but it may perhaps be too mild... The summer does not quite set in quite so abruptly as the winter. With an occasional hot day in October, it commences generally in November... On a normal hot summer day a sea breeze always sets in about noon on the coast, and reaches Perth about 2 p.m. The temperature then commences to fall, and the evening and night are delightfully cool and pleasant... The appearance of soft, watery cumulus clouds in the West, generally about sunset, announces the arrival of the welcome change... At night probably a few light showers, and we realise that a definite change has occurred."

Johnston (1848) remarked that "...the south-east trade or passage wind extends... from about latitude 10 to 20 degrees south, within which limits it blows powerfully, and with great steadiness, from April to October... During the hot season... the space between the [equator's] line and 10 or 20 degrees south, is occupied by the north-west monsoon, which then attains its southernmost limit... South of the zone of the trade winds, we find the district of the north-west winds..." Cooke (1901) confirmed that north of the tropic "the year may be divided into two seasons - wet and dry; the former lasting from the middle or the end of November to the end of March. During this period the weather is very unpleasant, the maximum temperature every day being close to or above 100°F (37.8°C), and records of 110°F (43.3°C) are by no means infrequent. [In a previous edition, Cooke had mentioned press telegrams, perhaps from Onslow, stating that "a delightful cool change has set in; the shade temperature has dropped to below 100 deg." (37.8°C) but this mention was omitted in 1905]. Thunderstorms, accompanied by heavy rain, are frequently experienced, and it is during this season that the willy-willy [tropical cyclone] occasionally visits the North-West coast. A moderate rainfall can generally be relied upon down to about latitude 20 degrees... In the winter months, or dry season, the climate is considered by the inhabitants to be most enjoyable..."

Early observations: South-West Africa

Monteiro wrote in 1875 that at Mossamedes (Moçàmedes, Angola, 15°15'S) "near the coast there blows a strong sea breeze from 9 or 10 hours until about sunset, often too strong to be comfortable... In the hot season temperatures rise to 22 or 24°C, rarely to 32°C. In the cool season it rises to 22 to 24°C, to fall nightly to

* Square brackets [] indicate words or sentences inserted to clarify the original text

15 to 18°C. The nights are so cool that for about six months one finds a blanket comfortable at night" (Hann 1910). At Tiger Bay (Bahía do Tigre, 16°45'S) Chun (1903) had found that Negro women preparing the fish ashore "wore sheepskin jackets for protection from the cool wind." At that time freshwater, totally lacking in the area, had to be brought in from Mossamedes.

Mühry (1862) quoted from the official 1842-56 observations, much more informative, particularly with regard to the moderate rainfall, the summer drought [which, as in Western Australia, extends throughout March as well] and the scarcity of thunderstorms. Dew is plentiful near the coast. The climate of Namibia (formerly German Southwest Africa) "is dominated throughout the year by cool southwesterlies, even stronger in summer. Ocean water at Walvis Bay has a surface temperature of 12 to 15°C and southwards to Angra Pequena 10 to 12°C, which explains the temperature of this coast, uniquely low for its latitude. The coastal land strip dominated by these cool winds is about 70 to 100 km wide. It is practically rainless, quite a desert, covered by sand dunes, which the frequent fogs moisten only superficially. The daily and annual range of temperature is narrow, the cloudiness brought by the frequent sea fogs is great. In contrast with this stands the climate of the interior... It is very difficult to shield the thermometer from radiation by the heated ground, walls in the sunshine, etc." (From a report in the *Petermanns Geographischen Mitteilungen* of 1894, quoted in Hann 1910). "The densest fogs, which can wet right through in a short time, are limited to a coastal strip some 30 km wide; further inland to a distance of up to 100 km from the sea they are less frequent and lighter; in the higher interior they are absent or very rare..." (Pechuël-Loesche 1886, quoted by Hann 1910). "Thunderstorms travel [from the interior] from East to West. While they move towards the sea, they never cross the coast, above which they dissolve. Walvis Bay had one thunderstorm in years... Swakopmund and Windhoek lie on the same latitude, and Windhoek at 1660 m of altitude is 4°C warmer than Swakopmund on the coast, in December and January some 6.7°C" (Hann 1910).

During a morning walk at Walvis Bay one noticed "still air, and a thick grey blanket of cold fog enveloping the beach. It dripped from the roofs like a gentle rain and the upper layer of soil is wet through, but a few centimetres below the surface it is dust dry... The humidity of the air reinforces the cold sensation... The fog dissipates before 10 or 11 hours and the sun breaks through. The horizon remains dusty and the extraordinary humidity by noon gives a muggy oppressive sensation, even while the thermometer rarely shows more than 25°C.... After sunset the fog rises again from the sea..." (Dove 1897, quoted in Hann 1910).

The hot dry winds (the *berg* winds) that descend from the interior to the coast "are not desert winds, but Föhn winds, which owe their high temperature to the descent of the air from the high interior..." (Hann 1911). They blow from late April to June and are "the most remarkable phenomenon of this whole coast as far as Port Nolloth... They warm the air up by 7 to 9°C and lower the relative humidity quite remarkably" (Hann 1911).

Early South African observations were quite fragmentary: Kaemtz (1843) for instance wrote that at the Cape of Good Hope [Cape Town Observatory] mean temperatures were: winter 14.8, spring 18.6, summer 23.4 and autumn 19.4°C. These values were based on 7 to 11 years of observations. "The average relative humidity reaches 74% for the year, the driest month (February) has 64%" (Lorenz & Rothe 1874). Hann (1911) wrote a good climatological description: "In Cape Town southeasterly winds dominate in summer, northwesterly winds in winter. In the summer half-year (October to March) the southeasterly reaches significant force and often blows for a week or two without interruption, stirring up masses of dust and making things very uncomfortable. On the other hand it is also a blessing, renovating the stagnant air in the hollow below the Table Mountain; it earns the name of 'Cape Doctor'... The force of the wind is so considerable and in summer it blows so persistently that in unprotected spots all tree trunks lean towards the North... Northwesterly winds dominate in winter; they bring moist air, thick clouds and the rainy season..." The greatest contrast in rainfall in southern Africa is between the exposed upper slopes of Table Mountain and Port Nolloth, also on the west coast.

Early observations: Western South America

Johnston (1848) published the observations made by A. von Humboldt in 1802: "The perceptible amount of cold which is felt in the tropics, a few feet above the surface of the ocean in the so-called Desert of Lower Peru, is owing to the low temperature of the sea, and the interrupted action of the sun's rays during the period of the garúa." Mühry (1862) quoted also from Humboldt: "the Antarctic Current [later renamed the Humboldt Current] brings a considerably lower temperature along the western coast of South America..." Lima's temperatures "are lowered by about 3° Réaumur [3.75°C] by the [thermal] anomaly of the Antarctic Current..." Duperrey in March 1823 found the air at Callao (Lima) to be at 20.2°C, about the same temperature as the ocean surface, and some 6°C cooler than the average air temperature at the same latitude (Johnston 1848); Johnston showed the 70°F (21.1°C) air isotherm west of Chile bent equatorwards by about 7 degrees of latitude and that of 60 °F (15.5°C) by about 9 degrees.

"As a result of the condensation of fog in the winter two annual seasons are distinguished, the aptly named colder overcast, from May to September, and the warmer clear sky, from October to May. In November one begins to see the stars, which remain visible until April; then appear the stationary fogs, *garúas*, and the solar disk remains yellow-red for weeks on end ; even in

summer it could so appear occasionally. This applies to the whole Peruvian coast, which receives no rain." From a note written by Humboldt in 1845 (also based on his 1802 observations and quoted in Johnston 1848): "The vapours of the *garúa* of Lima are so thick that the sun seen through them with the naked eye assumes the appearance of the moon's disc. They commence in the morning and extend over the plains in the form of refreshing fogs, which disappear soon after mid-day, and are followed by heavy dews which are precipitated during the night." Ships "at the time of the garúa... are unable for several days to obtain any observations for latitude; and, prevented by the fog from ascertaining their position on the coast, they are often... carried past the harbour... The mist and fog are most dense between Pisco [13°52'S] and Lima." Darwin (1839) wrote that in July 1835 "during our whole visit the climate was far from being so delightful as it is generally represented. A dull heavy bank of clouds constantly hung over the land, so that during the first sixteen days I had only one view of the Cordillera behind Lima... It had almost become a proverb, that rain never falls in the lower part of Peru. Yet this can hardly be considered correct; for during almost every day of our visit there was a thick drizzling mist, which was sufficient to make the streets muddy and one's clothes damp: this the people are pleased to call Peruvian dew." Lima is in the rain-shadow of the trade winds (Fig. 2) "which extends a further 40 miles over the ocean, and in consequence there are no storms on this coast." G. Birnie, ship surgeon, wrote in 1824 that the main characteristic of the coastal strip of western South America from 5 to 30°S (Payta to Coquimbo), about 370 miles long and only 14 wide, is "that no rain falls and the sun is mostly covered by a curtain of clouds (the latter as a consequence of the lower temperature of the Antarctic Current). Thereby this coast is a barren desert... The mean temperature may be estimated at 18° Réaumur [22.5°C]."

As to much of Chile in general, Mühry quotes Molina, whose work was published in 1782, saying that "northern Chile suffers its drought because of the persistent trade winds, with some indication of the transition from the tropical to the subtropical belt by cloud formations in summer and in winter; in the middle tract the subtropical belt takes over with winter rains and rainless summers... This long-stretching land is one of the finest in America, because of the clearness of its sky, the constant mildness of its climate... From the beginning of spring till the autumn the sky over the land between 24° and 36°S is constantly clear; there is seldom a year in which in this period even a light rain falls... In central Chile the rains begin in mid-autumn, *ie* in April, and continue through the winter till the beginning of spring, *ie* the end of August. The rains increase from North to South. In the northern provinces, Copiapò (27°S) and Coquimbo (30°S), they are scarce; in the central provinces however it rains three or four days without interruption, followed by 15 or 20 clear days... Thunderstorms are very rare."

When there is a break in the stratus cloud or fog, the intensity of insolation reverts to normal: "proceeding inland, warmth increases up to an altitude of over 300 m, particularly in summer" (Lorenz & Rothe 1874).

Of Iquique (20°12'S) Darwin (1839) wrote that "the whole is utterly desert. A light shower of rain falls only once in very many years... During this season of the year [winter], a heavy bank of clouds extending parallel to the ocean, seldom rises above the wall of rocks on the coast... Water is brought in boats from Pisagua, about forty miles to the northward... On the coast mountains, at the elevation of about 2000 feet [about 600 m], where during this season the clouds generally hang, a very few cacti were growing in the cleft of rock... Whatever its origin may be, the existence of a crust of a soluble substance over the whole face of the country, shows how extraordinarily dry the climate must have been for a period long antecedent."

In 1887 Ball (Hann 1910) wrote that at Tocopilla (22°10'S) "the view was absolutely that of a moonscape, a world without water", but at Antofagasta he was told that heavy rains fell once in 5 or 6 years [rains associated with El Niño?].

Copiapò (27°22'S) at 395 m "is every morning enveloped in thick fog which reaches as high as Pabellón, about 275 m higher, where the sky is always clear. One can only see some clouds very far to the West. Rain falls at Copiapó once or twice a year, often consisting of a few drops" (quoted in Hann 1910). Darwin (1839) had written that (at Copiapó) "after two or three very dry years, perhaps with no more than one shower during the whole time, a rainy year generally follows; and this does more harm than even the drought... Once for a period of thirty years not a drop [of running water] entered the Pacific. The inhabitants watch a storm over the Cordillera with great interest; as one good fall of snow provides them with water for the ensuing year. This is of infinitely more consequence than rain in the lower country. The latter, as often as it occurs, which is about once in every two or three years, is a great advantage... But without snow in the Andes, desolation extends throughout the valley." In the Andes "the winds of these lofty regions obey very regular laws: every day a fresh breeze blows up the valley, and at night, an hour or two after sunset, the air from the cold regions above descends, as through a funnel."

At Valparaíso in late July Darwin (1839) noticed that "after Tierra del Fuego, the climate felt quite delicious - the atmosphere so dry, and the heavens so clear and blue with the sun shining brightly, that all nature seemed sparkling with life... Here, during the summer, which forms the longer portion of the year, the winds blow steadily from the southward, and during the three winter months [rain] is however sufficiently abundant... I did not yet cease from wonder, at finding each day as fine as the foregoing."

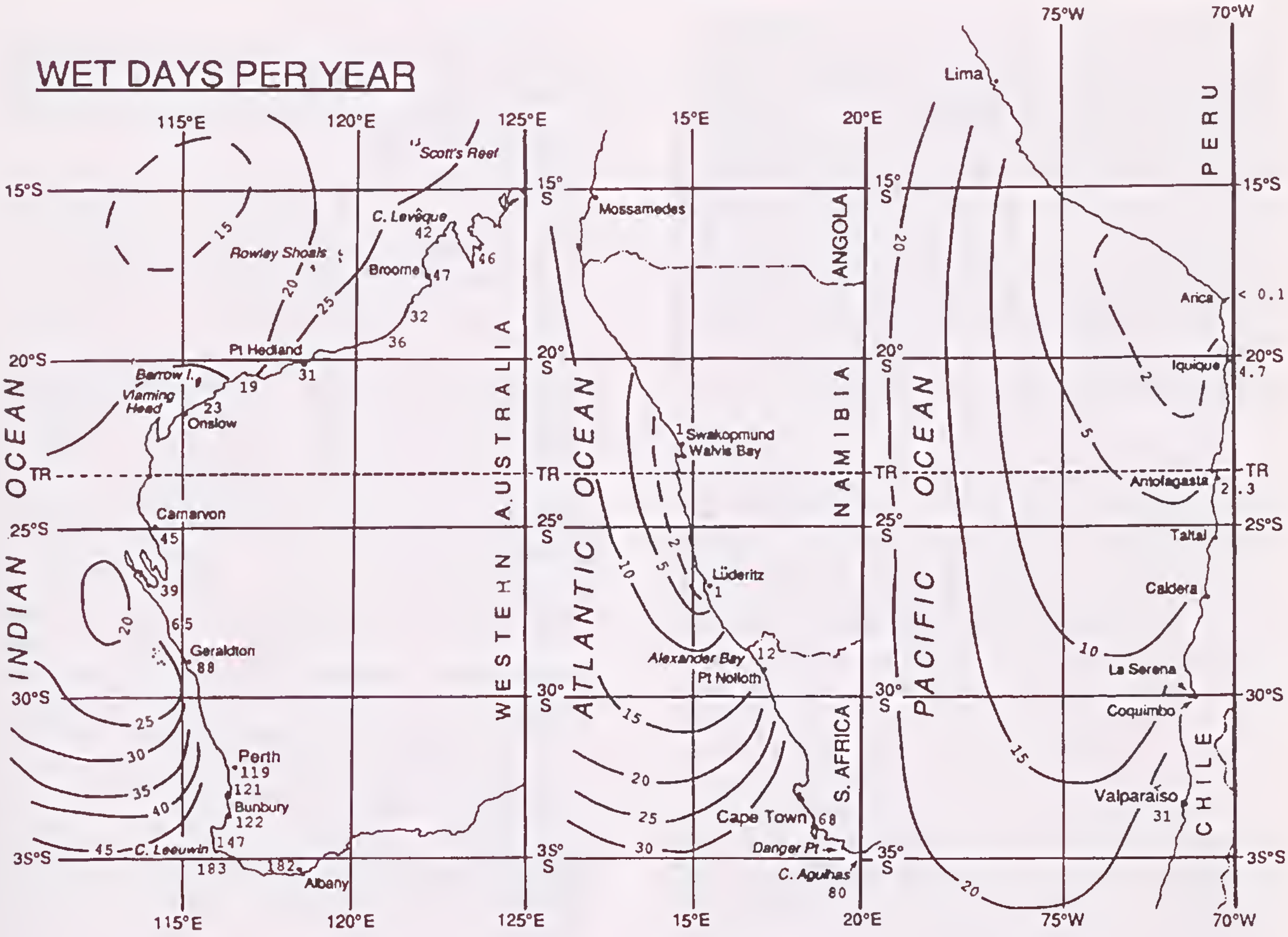

Figure 1 Outline of the regions studied and number of wet days per year offshore (from ships' observations) and at coastal stations.

Although these regions were treated in separate chapters, Hann (1910, 1911) used every opportunity to make penetrating inter-regional comparisons. The only modern avowedly comparative study of these climates is due to Lydolph (1957); good but separate evaluations are found in Trewartha (1961). Modern work with many maps on each region's climate is readily available in Schultze (1972) and Höflich (1984) for Africa, Miller and in part Johnson (1976) and Streten & Zillman (1984) for South America, and Gentilli (1971) and Ramage (1984) for Australia, besides many localised or specialised papers, most of which are referred to in the text and listed as references.

A hierarchy of climatic factors

1. *Planetary location.* The basic factor in this group is *latitude*, with the consequential seasonal changes in *insolation* and the many derived changes in temperature, air circulation, moisture mobilisation and transport, affected and modified by many factors further removed from the initial planetary pattern. By and large, these latitudes are principally influenced by subtropical anticyclones, which consist of descending and therefore dry air, eventually spreading equatorwards along the surface as the well known trade winds. In Hettner's (1930) genetic classification of climates these regions mainly have a dry trade-wind climate extending northwards to *ca* 8°S (over 2600 km) in Chile and Peru, 18°S (1200 km) in Namibia, and only 22°S (560 km from N to S) in Western Australia. At the southern margin (25 to 30°S) the anticyclones alternate seasonally with mid-latitude depressions; the anticyclonic winds dominate the hot season, which they contribute to make drier. From these winds' ancient name, Hettner called this alternating type of climate Etesian. The seasonal persistence and the alternations of wind regimes are clearly shown in a map by Köppen (1931), which gives a first basis for the differentiation of the three regions: western South America with the least modified trade-wind regime, southwest Africa where the trade winds are slightly deflected towards the coast, and Western Australia with wind alternations and modifications, and isobaric troughs (Gentilli 1969).

2. *Continental geometry.* The most significant differences between the three coastlines were outlined at the beginning of this paper (Fig. 1). Most important are the slanted very broad opening towards the equator north of Australia (which favours water exchange, Southern Oscillation impulse transmission and the development of monsoonal and pseudo-monsoonal air

circulations) and the extension of South America into the higher latitudes, leaving perhaps southern Africa, in this respect, as the intermediate 'norm'. Continental influences exaggerate both hot and cold thermal extremes and oceanic influences reduce them. Concave shorelines allow continental influences to affect the air further seaward (*eg* Eighty Mile Beach, Shark Bay, Walvis Bay and Alexander Bay), thus increasing temperature ranges; convex shorelines have the opposite effect, recorded on the many capes and few small islands on the continental shelf. At these latitudes western meridionally - aligned coastlines give rise to strong land- and sea-breezes, as mentioned in 5 below.

3. *Oceanodromy* (ocean flows). The great southward extension of South America intercepts the West Wind Drift, deflecting most of it towards the equator as a relatively cool current. The remainder is deflected polewards and only past 52°S resumes its course as a colder segment of the Drift heading towards South Africa. Off Namibia the southerly wind that drives the current probably causes and certainly entrains some colder water upwelling along the coast (see 5 below). Lettau, in an appendix to Johnson (1976), ascribes the ascent of deeper and colder water off Peru to the Ekman effect within the Humboldt Current; Streten & Zillman (1984) write that "the coldest water, off the shore of Peru, stems mainly from wind-induced upwelling". These ocean currents and upwellings effectively cool the coastal strips of both continents, making a shallow layer of overlying air cooler and most stable, and consequently almost rainless notwithstanding very high relative humidities (Fig.5).

Breuer (1974) shows the average annual boundary between prevalently stratiform and cumuliform clouds (respectively in stable southern and unstable northern air) on the west coast of South America from about 42 to 11°S. In the summer it moves slightly offshore and becomes much narrower from the tropic to 16°S, where it ends.

In Western Australia a NNW-SSE orientation of the coast prevails from 23°S, whereas it occurs from 18°S in south-western Africa, and only northwards from 18°S in South America (Fig. 1). The gap to the north of Australia, so vital for the dynamics of the oceanic circulation, indirectly has a very significant effect on climate, allowing warm Pacific water to enter the Arafura Sea during the Australian autumn and winter. "There lack on the west coast of Australia the cool ocean currents (and the upwelling cold water) which so effectively lower temperatures on the west coasts of southern Africa and South America..." (Hann 1911). Dutch ship observations of rare mists and fogs far off the West Kimberley coast and west of 108°E a long way off the Pilbara coast (Koninklijk Nederlands Meteorologisch Instituut, 1949) suggest occasionally contrasting water and air temperatures. The Cocos-Arafura ocean region has mostly clear skies and receives over 185 Wm^{-2} per year on 1,160,000 km^2 160 to 185 Wm^{-2} on another 2,175,000 km^2 and 135 to 160 Wm^{-2} on another 3,800,000 km^2. Off Peru and Chile, because of stratus and fog cover, the best annual average radiation intake is 135 to 160 Wm^{-2} over some 300,000 km^2 with the remainder below 135 (calculated from Gorshkov *et al.* 1974).

The general trend of the coast and the position of the anticyclones over the oceans to the west affect the impact or otherwise of the anticyclonic margins on coastal waters and coastal air as well (see 4 below).

4. *Orography*. The remarkable difference of forms between the three continents is shown in Fig. 2. The cross-section is taken along the tropic; on the western margin of South America the Andes are a very effective climatic barrier, crossed very seldom by weather disturbances from the Pacific, which lose much of their energy during the uplift (South African Weather Bureau, 1957-58). An important consequence of this barrier effect is that the surface winds from the South Pacific high-pressure system run northwards along the coast of South America, whereas the homologous winds from the South Atlantic system can spread for some distance inland, assuming a south-south-westerly direction over the Namibian coast. The rain-shadow effect of the Andes on any possible easterly air flow is enormous, and the desiccating effect on any air descending their slopes is noticeable, although other factors (para. 3 and 5) combine to cause the total dryness of much of the Atacama Desert. Every valley is swept by a westerly valley breeze in the morning and an easterly mountain breeze in the afternoon, which may continue as a land breeze at night; from the observations of Miller (1976) one would surmise the arising of true land- and sea-breezes diagonally across the shore and the western foothills of the Andes.

Both Australia and southern Africa have a raised rim on their eastern margin. The height of the African Plateau is sufficient to allow surface atmospheric interchange while increasing the contrasts between easterly and westerly weather systems, modifying both, strengthening any katabatic (Föhn) effect on descending easterlies and contributing to make the Namibian coast one of the most extremely arid regions in the world. One of its peculiarities is that in the cooler season, and particularly in May-June, these exceptionally dry and hot berg winds from the interior, heated adiabatically, make temperatures rise above 40°C and humidity sink to below 10% (Köppen 1931).

The low Western Australian Plateau allows free transit to weather systems, introducing only distance travelled overland and the interior's overheating as modifying factors and, where topography aids, a mild katabatic (Föhn) effect noticeable in hot summer easterlies and in the mean maximum temperatures at *eg* Nyang, Marble Bar, Gascoyne Junction. The significance of clear skies in the radiation budget may be assessed from 3 above.

5. *Hydrothermostasy* (thermal condition of water). Its distribution is directed by the movements of the water

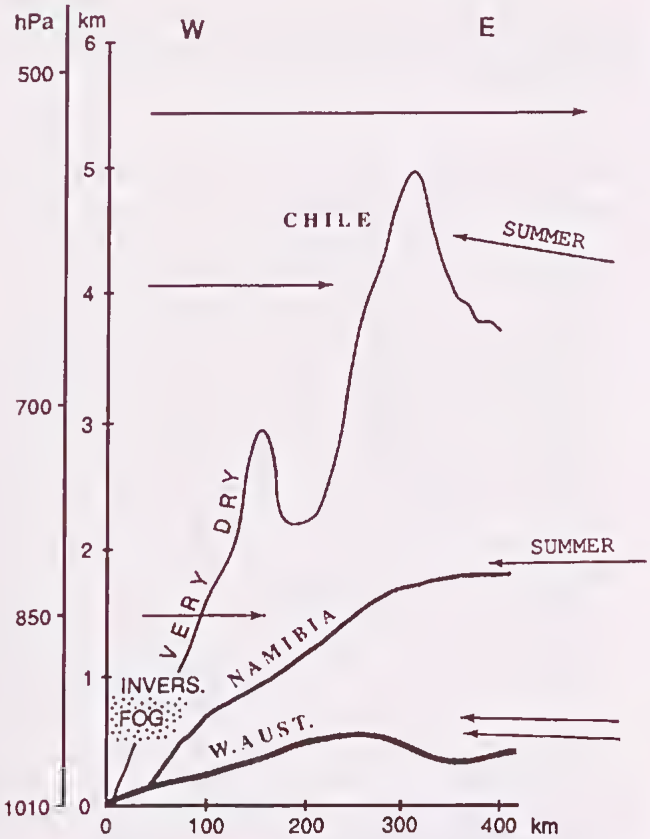

Figure 2 Cross sections of the three regions along the tropic, main seasonal winds, and average position of the inversion and the underlying fog on the Chilean coast.

masses as in 3 above, but the initial amounts of heat, the rates of change and/or dispersal and rises and falls in thickness and in level are also largely affected by solar radiation, evaporation, etc. Along the Namibian, Peruvian and north Chilean coasts the upwelling of cool ocean water is a very powerful climatic factor, cooling and stabilising the overlying air and thus preventing any convection (no thunderstorms), condensing most of the moisture into fog and almost preventing any fall of rain (Figs. 4 and 6). Near Western Australia south equatorial water stored (Gentilli 1972) and further heated in and around the Arafura Sea adds a considerable amount of heat and moisture to the overlying air, causing instability and thunderstorms (95 days with thunder at the former Kunmunya Mission, 15°25'S,125°43'E). The "El Niño" phenomenon which episodically conveys warm water along the Peruvian coast is well explained by Streten & Zillman (1984) who also list its occurrences in previous years, overlapping with Schott's (1932) much longer historical series. The occurrence of convective (cumuliform) clouds has been mapped by Matsumoto (1989) using their interception of longwave radiation; a regional differentiation clearly emerges, particularly with regard to Western Australia.

Atmospheric circulation

Fig. 3, drawn from NOAA 1988 data for Perth and Cape Town and 1984 data for Valparaíso, shows that at 200 hPa (*ca* 12,000 m) stratospheric winds (mostly of jet speed) blow stronger above Perth than above Cape Town or Valparaíso almost throughout the year, with notable gaps only in summer. The greatest difference is noticed from May to October and appears stronger between Perth and Valparaíso. This is confirmed by van Loon *et al.* (1971) who for July show at 200 hPa and 30°S a mean geostrophic zonal wind of over 52.5 ms^{-1} across Australia, 37.5 to 40 ms^{-1} off Namibia and between 32.5 and 35 ms^{-1} off Chile. Along 20°S the wind slows down to about 20 ms^{-1}; consequently, Western Australia experiences a most dramatic contrast between subtropical and intertropical latitudes. Perth has relatively windier springs and summers.

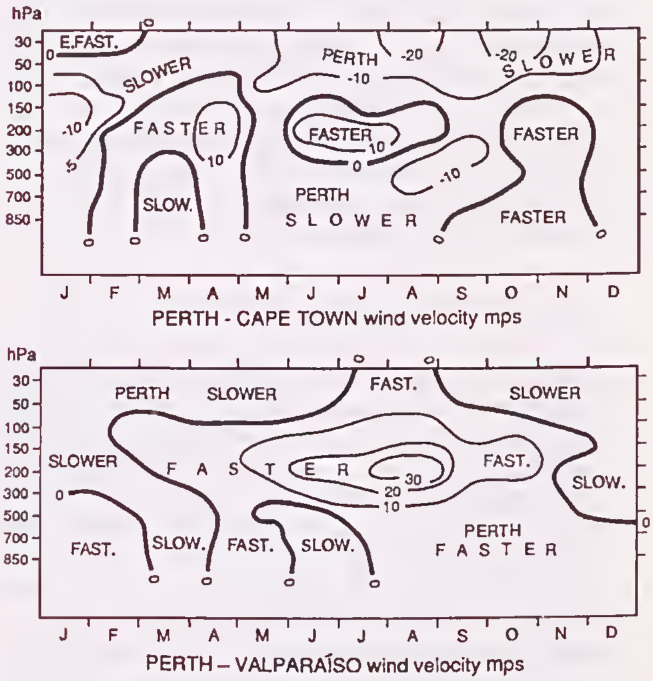

Figure 3 Difference in wind velocity, in metres per second, in the atmosphere up to 30 hPa (about 23 500 m) above Perth and Cape Town and Perth and Valparaíso respectively. Notice the 200 hPa belt where Perth is overflown by much stronger winds than the other two stations.

The descending trend of westerly winds is particularly noticeable from May to July, when isobaric heights above Perth are distinctly lower. At 500 hPa and about 25°S van Loon *et al.* (1971) show westerlies entering Western Australia at over 17.5 ms^{-1}, Chile at about 12 ms^{-1} and Namibia at 10 ms^{-1}.

Much of the additional energy in the atmosphere above the Western Australian coast derives from the additional solar radiation received, from a direct greater latent energy input (from the inflow of sub-equatorial waters) as well as storage (heat stored in ocean waters off northwestern Australia). Southwestern Africa and South America show the effect of energy sinks (loss of atmospheric heat to the cool water masses

off their shores).

West of the three land masses lie semi-permanent oceanic anticyclones which, subject to the latitudinal displacement normal with the seasons (see above), send persistent southerly winds along the shores. This effect is strongest in summer and weakest in winter, when it is overcome by the transit of frontal depressions, which occur in all three regions, but much more regularly and frequently over Western Australia.

These southerly winds are strongest along the Benguelan and northern Namibian shores (see historical part above). Writing on the absence of pelicans, Shannon *et al.* (1989) suggest that "it seems probable that the winds of the Benguela coast, apart from at a very few sheltered sites such as Walvis Bay, are simply too strong for these birds' aerial manoeuvres." As is normal within the anticyclonic periphery, they are quite shallow: McGee (1988) gives them a frequency of 41% at Cape Town, but shows them decreasing sharply with height, whereas nor'westerlies, which are 28% of surface winds, become increasingly frequent with altitude to at least 300 hPa (*ca* 9000 m), where they are totally dominant.

Monsoons, tropical cyclones and epitropical disturbances

Because of its configuration, Australia is the only southern land mass which gives rise to a monsoonal circulation, albeit a weak one. Particularly with regard to Western Australia it may be called a pseudo-monsoon (Gentilli 1971) because it is very shallow and seldom involves trans-equatorial air, which is the normal surface component of a full monsoonal circulation (although Ramage (1984) takes a seasonal 90° change in wind direction across a coastline as sufficient proof of a monsoonal circulation); most of the summer westerly flow into the Kimberleys, as clearly shown for instance by Ramage (1984) in his Fig. 16, is air from the high-pressure belt to the west of Australia, initially very dry because of its slow descent as part of an anticyclonic system, steered towards the Kimberleys by the northern margin of the almost stationary Pilbara low. Matsumoto (1989) writes that the Australian monsoon season, lasting about 80 days, "is the shortest among all continental wet periods in the tropics."

Fig. 4 shows the mean monthly rainfall received at each latitude: a large area including all the Kimberleys receives much of its rainfall, from December to March (the "wet"), from this pseudo-monsoonal circulation and thunderstorms. Matsumoto (1989) shows two parallel lines of low outgoing radiation in the Australian region, the main one (caused by truly monsoonal cloud systems) being just to the north of Australia, and the weaker one running from the Kimberleys to north Queensland.

Tropical cyclones need an ocean surface temperature of at least 28°C as a source of energy and a latitude sufficiently far from the equator to allow the Coriolis effect to initiate the rotation of the system. These requirements exclude them from southwestern Africa and South America, while allowing them to occur several times a year in Australia (Coleman 1971 and Lourensz 1977).

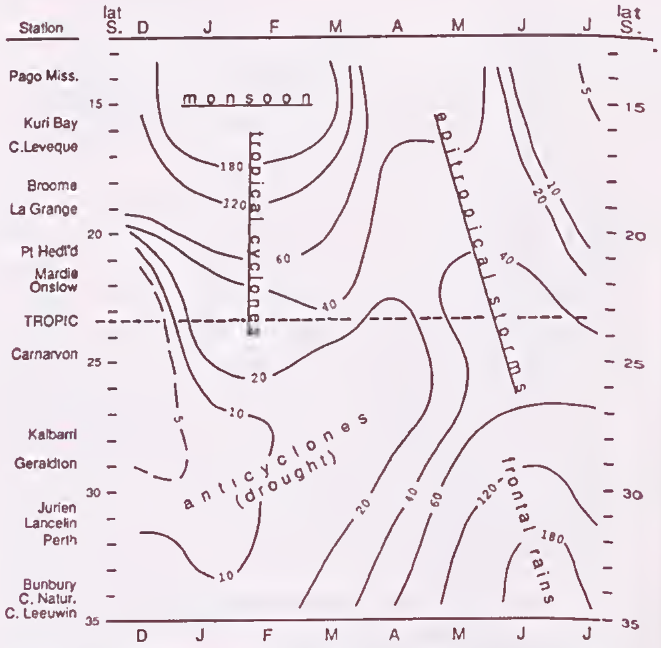

Figure 4 Chronolatitudinal graph showing the average monthly rainfall at coastal localities in Western Australia. The underlined rain-bearing systems (monsoon, tropical cyclones and epitropical storms) do not occur in southwestern Africa or South America.

The immense and concentrated energy of tropical cyclones transports enormous masses of water vapour to the subtropical latitudes, with occasional incursions into the middle latitudes. Fig. 4 shows this southward transport of moisture as mean monthly rainfall in each latitude; as far south as Broome the contributions of monsoons and cyclones may differ little in overall quantity, but cyclones are far less frequent and infinitely less reliable. Their average annual contribution to Western Australian rainfall (mostly restricted to a few days in January) ranges from some 400 mm in the northern Kimberleys to 200 mm at Broome and just under 50 mm at Carnarvon (Milton 1978). In practice, averages are almost meaningless when cyclones are concerned: in an arid region one cyclone may bring half the mean annual rainfall in three or four days.

Epitropical disturbances are peculiar to Western Australia (Gentilli 1973, 1979a). They mostly occur from May onwards, when the water at lower latitudes is not warm enough to start a tropical cyclone. The uplift of moisture is usually provided by massive thunderstorms over Indonesia or the Arafura Sea, or occasionally by a tropical cyclone. Tapp & Barrell (1984) plotted the 'tropical extremities' of 53 'North-West Australian cloud bands' (the present official label for the phenomenon) between September 1978 and August

1982 inclusive and found that 25 appeared between 7°30' and 12°30'S and 87°30' and 112°30'E. They are conveyed below the subtropical jet stream (belt of strongest winds in Fig. 3) and travel southeastwards as 'upper air disturbances'. The amount of rain which they can bring varies, but is sufficient to make May wetter than April or June over most of the Pilbara, and to give many localities a secondary peak of rainfall in that month (Fig. 4). Tapp & Barrell (1984) counted 6 such events in April, 8 in May, 10 in June, 8 in July. The frequency of these epitropical disturbances varies from season to season and year to year, mainly according to the frequency of strong subtropical jet streams. They often only show the well described 'cloud band' of satellite images (Downey *et al.* 1981, Tapp & Barrell 1984, Kuhnel 1990) and may be the cause of slight changes in long-wave radiation emission between Exmouth and Port Hedland in Matsumoto's (1989) April and June records. Their average contribution of rainfall to Onslow or Mardie, about 40 mm a month, may seem to equal that from tropical cyclones, but in reality cyclones may occur once or twice a season while epitropical disturbances may transit every week, particularly in late autumn and early winter.

No such phenomena occur in Africa or South America. However, Harrison (quoted by Tyson 1986) identified the South Atlantic cloud band associated with a cyclonic poleward tract (accelerating) at 200 hPa (about 11,000 m) between about 18 and 35°S. As in Australia, the anticyclonic bend in the subtropical jet stream rises and slows down, and the cloud band disappears, to reappear again, as over Australia, after the next cyclonic poleward bend. It is suggested here that a most significant difference in the sequence over the two continents is due to the presence of the slightly warmer water in the eastern Indian Ocean: the jet stream increases in speed already before its entry into Australia (van Loon *et al.* 1971), whereas it slows down before entering South Africa. As a result, the wavelength of the meanders is shortened and their amplitude is increased over Australia. Over southern Africa the longer meanders make the cloud band reappear over the warmer Indian Ocean, and the shorter ones pass over Namibia without any visible cloud band (Harrison, in Tyson 1986).

Cloudiness, humidity and rainfall

These regions are unusual because some of their cloudiness is not associated with precipitation. A regional difference is already clear in a map by Hann (1896) with cloudiness varying strongly with latitude off Peru and Chile, moderately so off Namibia, and varying more with longitude off Western Australia. Samoilenko (1966) shows the waters off southern Peru and northern Chile with a July cloudiness of 6.4 to over 7.2 oktas where the rainfall for the month is under 5 cm with a probability of less than 5%. This is due to the steady inversion overhead which prevents the moisture below from rising, maintaining a relative humidity around 80% for the year (Száva-Kováts' map, in Blüthgen 1966). Off Namibia and South Africa the average relative humidity is over 70% with a July peak of 80% at Port Nolloth, which has minimal cloudiness and a total annual rainfall of 64 mm. Humidity decreases very rapidly towards the interior.

Off Western Australia, from Port Hedland to Derby (excluding Broome), July cloudiness is below 1.6 oktas (measured by nephanalysis, Ramage 1984) and relative humidity is below 50%. North of 30°S it still is less than 70%; fogs are rare, cloudiness and rainfall vary in nearly direct proportion. In respect of atmospheric moisture, Western Australia may truly be considered the most 'normal' of the three regions.

This 'normality', in a predominantly continental environment, leads to greater daily ranges of temperature, which in turn cause relative humidity to vary very widely. While the 3 pm observations are fairly close to the daily RH minimum, the 9 am observations are already - and specially in summer and with hot weather - below the daily RH maximum. The Council for Scientific and Industrial Research (1933) and the Bureau of Meteorology (1956) published mean relative humidity values, but these were omitted from later publications in which, at best, 9 am and 3 pm values are shown.

The three regions differ considerably in the amount of precipitation they receive (Fig. 5). In Western Australia the incursions of moist tropical air from whatever source bring large amounts of water vapour which may be condensed and released in very heavy showers (Walpole 1958). A mean rainfall intensity of 15 mm per wet day occurs where more tropical cyclones cross the coast between Port Hedland and Onslow [but there are very few wet days!]. North of the tropic the mean rainfall per wet day varies between 10 and 15 mm, decreasing further south to less than 5 mm on the south coast. South of the tropic, mid-latitude depressions bring most of the rain, apart from tropical incursions of cyclones and disturbances mentioned above.

In southern Africa heavy falls are brought by eastern weather systems, but much of the moisture is reabsorbed in the descent from the plateau. Occasionally depressions "which developed over positive sea-surface temperature anomalies in the south-east Atlantic Ocean" (Walker & Lindesay 1989) bring heavy rains; rainfall is increased at first by the gradual rise over the plateau as the fronts progress inland (Weischet 1969).

In South America the Andes interpose an impassable barrier to any rain-bearing system from the eastern side of the continent; the rare falls from southwesterly fronts are usually very light. An outstanding peculiarity of the South American west coast is the occasional occurrence of El Niño, a warm, southward current which flows temporarily between the cool Humboldt Current and the coast, rendering the overlying air humid and unstable and causing very heavy falls of rain, amounting to more than the annual average within a few wet days (Conrad 1936).

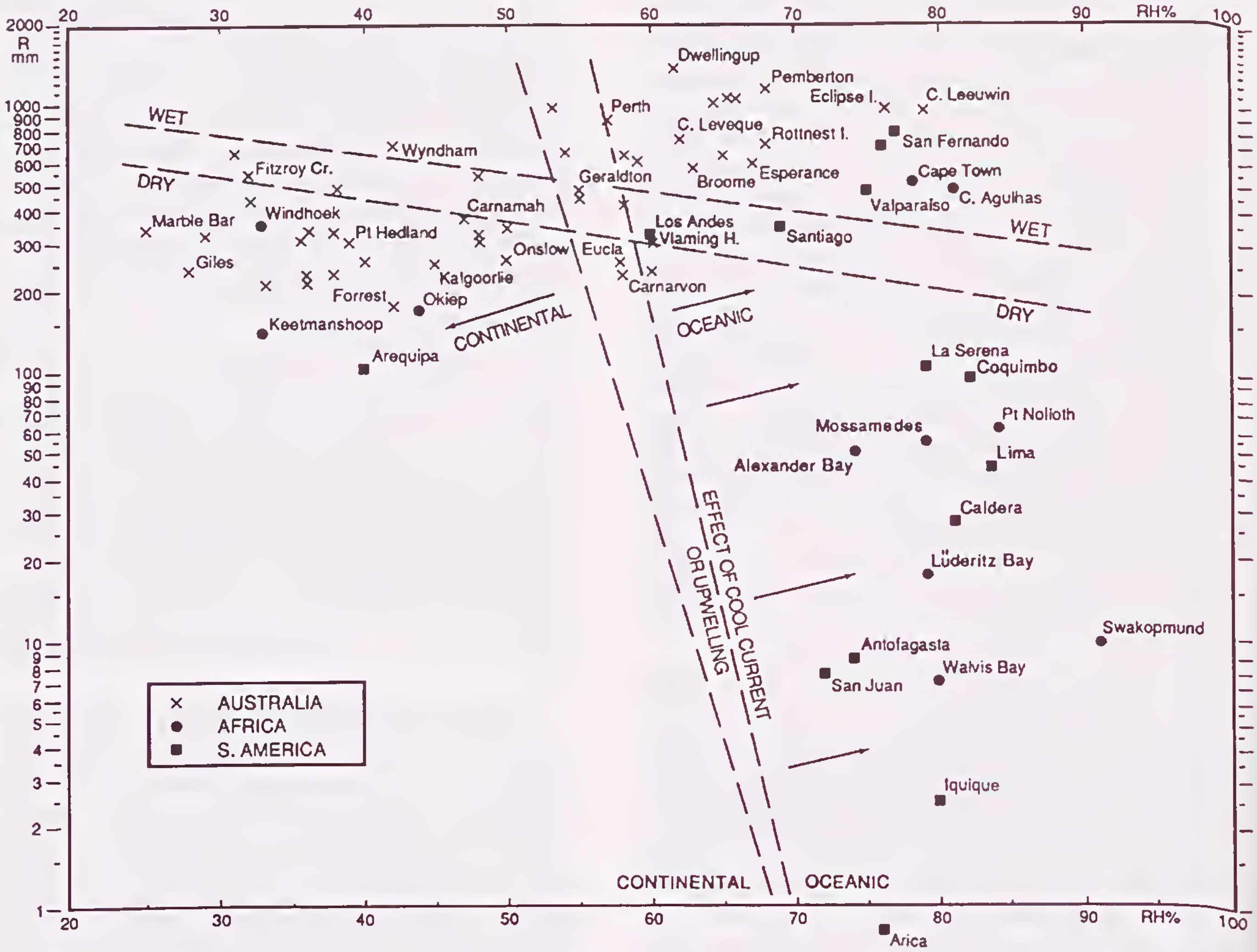

Figure 5 Regional differentiation by combined annual rainfall totals and annual average relative humidity. The graph (with a logarithmic scale for rainfall) shows the opposing continental and oceanic influences and the extraordinarily high relative humidities brought about by cool coastal waters.

The disastrous consequences of El Niño at sea are very well known, but floods and landslides in a normally very arid land also cause damages and losses. The effect of the warm Leeuwin Current on coastal rainfall is minimal because of the very limited surface of warm water involved; the relatively good rains on the Australian west coast are rather due to the absence of cool waters as affect the other two regions.

It is not possible to measure rainfall at sea from a moving ship, but it is possible to observe it. Most maps of estimated precipitation at sea are highly generalised; however, the maps in Schott (1935, 1942), Blüthgen (1966) and Korzun *et al.* (1974) show a clear regional differentiation. A narrow area under 100 mm a year includes the Peruvian and Chilean shores from about 8 to 30°S. Schott (1935) shows a narrow coastal strip under 10 mm (the Atacama Desert) running from about 17 to 25°S; Drozdov, in Korzun *et al.* (1974) shows it more restrictively from 20°S to the tropic. In Angola and Namibia the 100 mm isohyet encroaches over the land from about 18 to 30°S (Namib Desert). These maps differ considerably in the Australian region. Schott (1935) shows the annual rainfall gradually increasing westwards from less than 250 mm at Sharks Bay to over 2000 mm in Madagascar; Blüthgen (1966) shows an area with less than 100 mm per year, only about 6 or 7 degrees wide in latitude, situated off Western Australia and not affecting the coast, and less rain in the interior; Drozdov estimates the rainfall of the same area off Australia, like Schott (1935) linking it closely with rainfall over the land, but ranging westwards from under 400 to over 800 mm per year mid-ocean.

The data published by McDonald (1938) showing observations of 'rain in whatever form' at sea have been reworked here and converted to show the mean number of days per year in which rain has been observed (Fig. 1). Official data on the number of days per year with rainfall >1 mm have been shown for the coastal stations, although exact comparisons are not always possible because of the different definitions of wet day (with precipitation = ≥1 mm metric, ≥ 0.01 inch earlier British and U.S.A., with no possibility of conversion, affecting Australian and South African data). Simultaneous observations at sea at Greenwich

noon lead to some underestimate in the African region. However, the contrast between the three continents is most remarkable: Arica (Chile) has an average of 0.1 wet days per year, Swakopmund and Lüderitz (Namibia) 1 day, Mardie and Onslow (Western Australia) 19 and 23 days - mostly supporting Korzun's interpretation of the rainfall pattern. Over the area of coastal waters shown, the number of wet days per year rises only to about 20 off Chile, 30 off South Africa, and 45 off Western Australia. Furthermore, the number of wet days on the coast near 35°S is about 1.5 times its offshore counterpart in Chile, twice its counterpart off South Africa and about 3 times its counterpart in Western Australia.

An important regional difference is due to the 'sweep' of rain-bearing systems. Each kind of system - monsoon, tropical cyclone, epitropical disturbance, extratropical front - has a characteristic way of advancing, while at the same time being partly steered by adjoining pressure patterns. In Western Australia they arrive unaffected by colder ocean surfaces to the west or, if coming from the north-west, strengthened by warm water surfaces, and proceed inland almost unimpeded by orographic factors. In Peru and Chile the Andes intensify any fronts from the Pacific at first impact, but eventually fracture and often destroy them; on the Andean foothills Darwin (1839) observed the extreme localisation of a violent rain storm. Shannon *et al.* (1989) write that "rainfall in 'average' years in the Namib normally occurs as 40-50-km-wide storm cells, and not over broader fronts. Consequently, rainfall events are extremely patchy in their dispersion both in space and time."

A good comparison of seasonal rainfall patterns in these regions may be made from Fig. 6, which at first sight appears somewhat forbidding. The average monthly rainfall is shown for three stations in each continent: Perth, Cape Town and Valparaíso in the outer subtropical belt, Vlaming Head, Swakopmund (Namibia) and Antofagasta (Chile) near the tropic, and Cape Leveque, Mossamedes (Angola) and San Juan (Peru) in the intertropical belt. The rainfall is shown on a logarithmic scale to do justice to the highest and lowest amounts as well, and to show rates of variations in their true proportions.

In the outer subtropical belt the three cities receive similarly plentiful amounts of rain from May to October, but Valparaíso has a much drier summer. In the epitropical situation, the rainfall of Vlaming Head shows two peaks, due to tropical cyclones in January-March and to epitropical storms in May-June, as well as to fronts of well developed mid-latitude depressions in June and July. By September the anticyclones dominate the weather and rains are negligible. At Swakopmund the only average rains worth mentioning range from 1 mm in November and January to 2 mm in February, March and April. Antofagasta fares even worse, with 2 mm in June and less than 3 mm in July.

The most succinct statement of these peculiarities is probably still Hann's (1896): "Remarkable is the scarcity of rain on the western coasts of continents in the subtropical, in part even in the tropical latitudes,... from central Chile and as far as Ecuador, the western coast of southern Africa from the River Orange to as far as Benguela... The dryness of these regions depends on the atmospheric pressure... which brings dominant cool winds from the higher latitudes, and similarly also cool ocean currents, flowing in the same direction, which cool the coast... The stronger and more constant these air and ocean currents..., the more extreme the scarcity of rains..." The role of cool upwelling water was not yet known.

In the main, the statistical variability of rainfall is a function of its scarcity, or rather, of the likelihood of rain-bearing systems penetrating a given region; the drier the region, the less often is this likely to happen, hence a higher variability. Biel's 1929 map is highly generalised; it clearly shows the coastal areas of highest (>30%) variability as extending from about 10 to 35°S in Peru and Chile (La Serena 59%) and from about 12 to 28°S in Angola and Namibia (Walvis Bay 33%). A biologist (Seely 1989) writes that "rain is unpredictable" in the Namib desert. On the Western Australian coast the belt with such high variability runs only from 20°S to the tropic, much of it due to tropical cyclones which cross the coast, Mardie being situated on "cyclone alley". Just outside this limited belt, Onslow has a 26% variability, contrasting with reliable Geraldton's 14% and very reliable Perth's 8%.

Other forms of precipitation and turbidity

Important differences between the three regions emerge from an examination of the different types of precipitation and related or in some way similar phenomena. A problem is the counting of days with drizzle, specifically recorded only in northern and central Chile. There are also vocabulary problems affecting the description of fog-related phenomena in some languages (*eg* Meteorological Office 1939 and Zimmerschied *et al.* 1962). Some climatologists (Köppen 1931, Conrad 1936) also refer to possible observer's subjective influences on visibility records during fog, mist and haze.

Drizzle (*llovizna* in Spanish, the drizzling fog popularly known as 'Scotch mist' [but see below under fog]) consists of droplets between 0.2 and 0.5 mm in diameter, *ie* too small to be counted as rain. The table shows that in northern Chile, where its occurrence is recorded even though it cannot be measured, drizzle (loosely called garúa in the Andean region) is by far the most frequent form of precipitation; it is least common at Antofagasta (23°39'S) with only 0.6 days per year. From there it increases slightly northwards, and much more markedly southwards, until south of Coquimbo it gives way to definite and measurable rains.

Fog and mist are often confused and the distinction is rather conventional. *Mist* (with visibility over 1 km) is called *neblina*, also *bruma*, especially at sea, and at times *niebla* or *calina* in Spanish, *Nebel* or *feuchter*

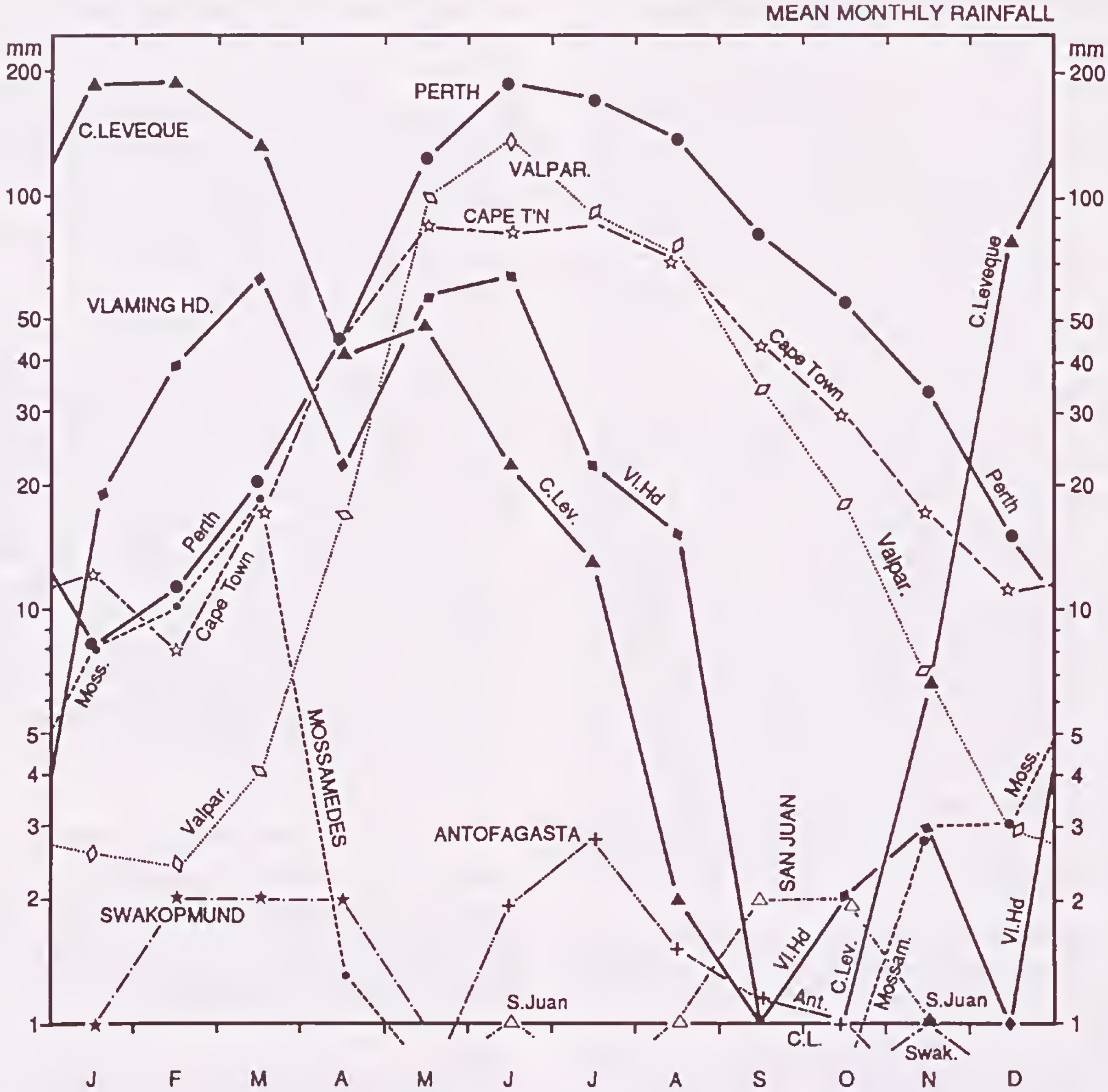

Figure 6 Mean monthly rainfall at Cape Leveque, Vlaming Head and Perth (Western Australia), Mossamedes (Angola), Swakopmund (Namibia) and Cape Town (South Africa), and San Juan (Peru), Antofagasta and Valparaíso (Chile). Note that the scale of monthly rainfall (in mm) is logarithmic, with the base line set at 1.

Dunst in German, *nevel* in Dutch. It is not recorded separately on the land, where it may be counted as fog with better visibility, *eg* in the Australian records analyzed by Maine (1968). It is strongly affected by the time of observations. *Fog*, with visibility under 1 km, is formally called *niebla* in Spanish, *Nebel* in German, *mist* in Dutch. The estimated frequencies of fog from marine observations just offshore are shown in Table 1 as Fog I, those at land stations as Fog II. Fog (or low stratus cloud when it is above the ground) is a major element in the climate of Namibia and Peru and central Chile, contributing a very high relative humidity (daily averages of 75 to 90 % every month) and reducing the amount of sunshine received along a coastal strip some 30 km wide in Namibia, narrower and more broken in Peru and Chile. In Namibia it may penetrate further inland: Brain (1988) during six summer weeks recorded three penetrations of fog some 100 km inland, all within five days. Its main cause is the cooling of the air and the condensation of its moisture content over the colder coastal current or even more so over the upwelling ocean water, or of warmer air advected over surface air cooled by the underlying water. It is suggested here that the initial fog may be denser and more persistent where upwelling ocean waters are cooler than the already cool surface waters, but in hot climates partial evaporation of water droplets results in the much finer garúa.

Table 1.
Yearly number of days with precipitation and allied phenomena.

Lat.	Chile						Namibia, S Africa				Western Australia					
S	Rain	Dr'zle	Mist	FogI	FogII	Haze	Rain	Mist	Fog	Haze	Rain	MistI	MistII	FogI	FogII	Haze
15	5	30	14	7	-	23	6	5	4	38	25	0	3	0	10	9
20	2	1	13	5	0	27	7	6	15	42	23	0	0	1	2	11
25	7	40	13	7	6	25	2	7	19	37	22	8	0	1	0	16
30	15	45	16	9	28	27	15	8	20	30	25	0	1	0	1	10
35	37	n.a.	17	12	54	26	30	9	11	25	50	0	4	3	5	7

Source: Days with rain, mist, fog I and haze calculated as close onshore as possible from McDonald (1938); days with drizzle and fog II for Chile from unpublished official data (Oficina Meteorológica de Chile) averaged from the nearest coastal stations; fog off Africa calculated from Deutsche Seewarte (1944); mist II and fog II in Australia calculated from Maine's (1968) data for Port Hedland and Onslow, Carnarvon, Geraldton and Perth. Fog II for 15°S (Beagle Bay and Broome) and 35°S (Cape Leeuwin) estimated from Loewe (1944). See text for consequences of standardised time of observations at sea.

In western South America there are terminology problems. Blüthgen (1966) quotes Knoch (1930) who describes the garúa as "hovering droplets hardly impeding visibility, with a tendency to accumulate locally, fairly evenly distributed throughout the year". Trewartha (1961) still describes it as a drizzling fog. Conrad (1936) accepts that garúa is clearly distinct from ordinary fog because it behaves differently, "being almost colloidal and - unlike fog - distributed unevenly among unsaturated patches of air". Sekiguchi (1986) defines garúa in northern Peru as 'dry fog': "We are driving a car, the sun is shining, visibility is good and distant scenery is clearly seen - yet the wind-shield gets wet. A film of water covers it. We have to operate the wipers. The black asphalt on the road becomes shiny. If we stop the car and touch it, it is wet... No large fog particles are floating in the air... The relative humidity exceeds 80% every day. In the morning, it is more than 90% almost throughout the year..." The problem is due to the difference in temperature between the land in the daytime and the surface of the sea. The atmosphere over the sea is almost saturated with water vapour. If the saturation vapour pressure of this air is 12-22 mb [hPa] and this air spreads overland, its relative humidity decreases to 50-60%, because the temperature of the coastal area is about 27-28°[C] and its saturation vapour pressure is 37-38 mb [hPa]. Therefore, water evaporates from the fog particles floating in the atmosphere and the particles get smaller. On the other hand a quotation in Knoch (1930) described the garúa at Lima as a fog copious enough to condense in fine droplets, forming a layer some 50 m above the water and 700 to 800 m thick, driven by the southwesterly wind against the seaward slopes. Lima at about 130 m is right in the fog, while its port quarter of Callao remains clear (Fig. 2). By garúa weather the air oozes moisture, umbrellas are quite useless, and the sun may not be seen for months. On the other hand at an altitude of some 800 m one is above the stratus layer and in bright sunshine. Sekiguchi (1986) writes that "the weather of Lima..., because it is enveloped by ordinary fog in the morning the year round, is humid and unpleasant. However, most days the sun shines in the afternoon, the fog turns into garúa and the humidity comes down to 60-70%. It scarcely rains... To avoid this strange and unpleasant climate, people of upper class families send their children to the winter resort Chosica 50 km east of Lima in the foothills of the Andes Range to give them more sun and light. The season of this winter resort is from May through October, when there are many cloudy days... During this season the schools are open."

In southern Peru and northern Chile the dense fog locally known as *camanchaca* (but recorded as *niebla*) is very significant particularly over coastal waters. From about 30°S Chile's long coastal strip is subject to very frequent normal fogs, also recorded as *niebla* (Fog II in Table 1).

Dew, mostly nocturnal and often overlooked by observers, may be the only or the main source of surface moisture in dry regions. From a 1925 paper by Hellmann, Conrad (1936) quotes annual totals of 176 days with dew at Coquimbo and 219 at Los Andes, both in Chile but respectively below and above the inversion layer; the Coquimbo record might be slightly inflated by observations of moisture left behind by early-lifted fogs.

Haze (*calina* or *bruma seca*, popularly also *neblina* in Spanish, *trockener Dunst*, often plainly *Dunst* but at times also *Nebel* in German, *nevel* in Dutch), mostly caused by dust or salt particles, is not a form of precipitation. It is normally carried over these regions by dry offshore winds. The table shows that it is frequent off Chile, and even more frequent off Namibia, which both have very arid coasts and practically no plant cover at these latitudes. Its frequency off Western Australia, where aridity is less extreme, is much lower and shows a definite maximum near the tropic.

Seasonality of precipitation

At the northern end of the three regions (15°S) rain at sea is more frequent in summer, but the frequency

ranges from 12% of the observations in Western Australia (with notable contributions from monsoons and tropical cyclones, Fig. 4) to 6.5 in Namibia and only 1% in Chile, where the Andes are a forbidding barrier (Figs. 2 and 6).

About 20°S summer rains are still noticeable in Namibia and Western Australia, whereas they are negligible in Chile. From this latitude southwards winter rains become more frequent in Namibia, and even more so in Western Australia, where they become dominant and reach 15% of the observations.

At latitudes 25 to 30°S regional differentiation becomes even more pronounced, with moderately frequent rains being concentrated in the winter in Chile, spread to winter and spring in Namibia, and most abundant from late autumn to early spring in Western Australia.

The transition to mid-latitude climates with more uniform rains may be seen at the southern end of each of the three regions where the percentage of rainy days in each season, beginning with summer and with the winter percentage in italics, is about 4+7+*22*+8% of the observations in the four seasons off Chile, 5+8+*11*+7% off South Africa, and 5+10+*21*+15% off Western Australia. These values may be compared with the monthly averages for coastal land stations in Fig. 4.

Mist is not frequent, and may be observed in any season off Chile, more in spring off Namibia, and, though uncommon, mostly in winter off the Exmouth Peninsula (mist I in Table 1) and on the Western Australian coast (mist II, usually merged with fog data).

Although the theory of its formation is very well known, fog is so closely affected by the conditions of the underlying surface (and some subjective judgment by the observer, for example Köppen 1931, Conrad 1936) that observations present many practical difficulties, including the timing of the observations themselves because fog is so readily dissipated by thermal and dynamic factors, being very frequently a nocturnal and early-morning phenomenon which on land would most often escape the Australian 9 am observing time, and certainly in summer even the South African 7 or 8 am observations. At a land station, even a short period of fog any time in the 24 hours should result in a "day with fog" being recorded. Noon at Greenwich (the time of observations at sea) corresponds to about 7:30 h off Chile, 13:00 off Namibia, and 20:00 off Western Australia, leading to a fairly adequate assessment of "days with fog" off Peru and Chile (where Blüthgen (1966) shows over 40 days per year between about 18°S and the tropic, fewer further south), a greatly reduced assessment except in winter off Western Australia, and an almost total exclusion off Namibia, where on the other hand Blüthgen (1966) charts over 80 days with fog per year.

The glaring differences between sea and land (Fog I and Fog II) observations in Table 1 show just one example, or perhaps one result, of these difficulties. Fog occurs moderately throughout the year, but more often in autumn and winter, off Chile. It forms more readily onshore and is a semi-permanent feature at altitudes of a few hundred metres on the slopes of the Andes (Fig. 2). It is more frequent in autumn and spring off Namibia (Deutsche Seewarte 1944), but after a specialist workshop at the end of 1988 Shannon *et al.* (1989) could still write that "even the formation of fog was shrouded by ignorance and clouded by speculation." The same workshop stated that "research on fog formation, movement and chemistry in the Namib-Benguela is necessary in view of the important role which fog plays in the system. Even at a very basic level, the contribution that upwelling makes in fog generation and in the maintenance of the aridity of the Namib needs to be established."

In Western Australia fog is uncommon, and at sea almost exclusively an autumn phenomenon (summer and early autumn according to the very detailed maps by the Koninklijk Nederlands Meteorologisch Instituut 1949). Onshore the very infrequent fogs occur mostly in winter and early spring (Maine 1968); there is a secondary peak in February at Carnarvon, March at Onslow, Geraldton and Perth, and April at Port Hedland. At Geraldton winter has few days with fog, and the main peak is in September-October.

Haze, generated by dry conditions and therefore affected by the timing of observations in almost the opposite way to dew, is recorded more frequently in the summer off Chile and Western Australia and practically throughout the year off Namibia, with a maximum in the autumn. Shannon *et al.* (1989) advocate research into its contribution of minerals to offshore waters. Off Chile the distribution, apart from the summer, is relatively even throughout the year, whereas in Western Australia the frequency and abundance of rains prevent the mobilization of dust once the summer drought is over. However, Keough (1951) gives an annual average of about 3 dust storms for Geraldton (adding that "dusty conditions are more frequent in late summer with NE to SE winds") and about 5 for Port Hedland. At Carnarvon "dust storms occur occasionally and dust often accompanies the onset of SSW breeze". At Kalgoorlie "dust storms occur on 13 days per year." The recording of the far more frequent dust haze is obviously inadequate, as is that of smoke haze in the South West.

Upper air correlations

A pilot study of some upper air comparisons, based on NOAA's Climatic Data for the World, was shown in Fig. 3. A very significant factor in the formation of rain is the dew point, of which upper-air cross-sections are given in Fig. 7. It should be noted that Australian observations do not extend above 500 hPa.

Regional differences stand out very clearly. Above Perth there is a gradual transition from 2°C at the surface in June and early July to 15° or 20°C at 700 hPa (about 3000 m). Above Cape Town a surface average of

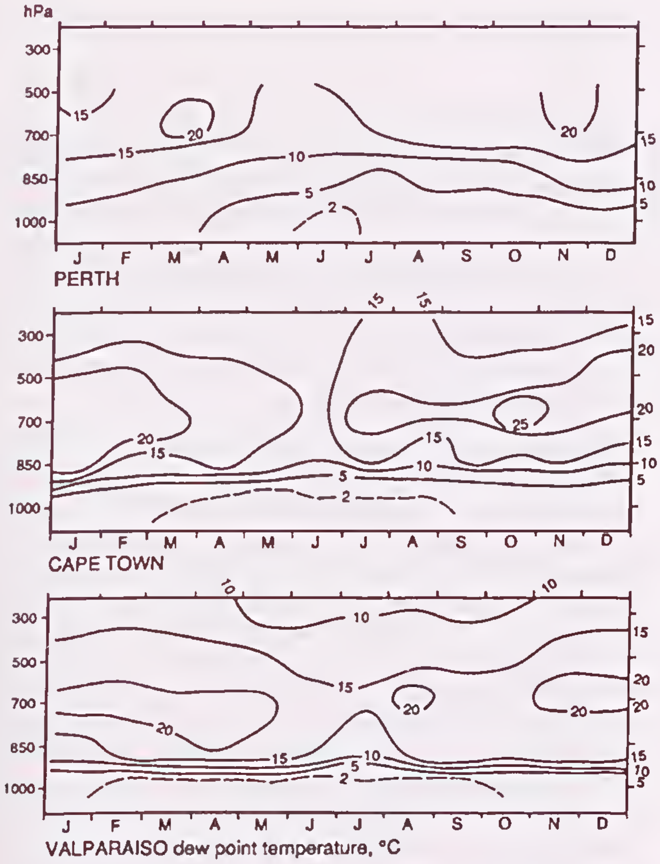

Figure 7 Dew point temperatures above Perth, Cape Town and Valparaíso. Notice the differences: very smooth change with altitude above Perth, rapid change from 5° to 10° and at times 15°C above Cape Town, and rapid change from 2° to 15°C (from below to above the inversion) above Valparaíso.

less than 2°C lasts from March to early September, but in altitude temperatures above 20° are far more prevalent, both vertically and seasonally, than above Perth. Above Valparaíso a marked atmospheric stratification is evident, with isotherms running parallel or nearly so at most heights: the surface dew point is below 2°C from February to mid-October, while dew points above 20° are mostly confined to the 700 hPa band.

The most significant difference between the three stations is in the stratification below 1000 m (well below 850 hPa): as the figure shows, this stratification is non-existent above Perth, continuous but with a range of some 5°C above Cape Town, and even more solid, with a range of some 10° to 13°C, above Valparaíso. This is evidence of almost permanent atmospheric inversions, particularly above Valparaíso, which prevent convective activity - thunderstorms and hail have hardly ever occurred at some Chilean stations.

Upper air and rainfall relationships

A preliminary survey was undertaken of correlations between conditions and movements of the upper air and monthly average rainfall at the underlying stations. A small part of the results is given in Fig. 8, which shows correlations (R^2) between each station's actual monthly rainfall and the upper air conditions or movements for the same month, for the month before, and for two months before. To the left are the correlations with upper air temperature, to the right those with geostrophic wind speed at the various levels.

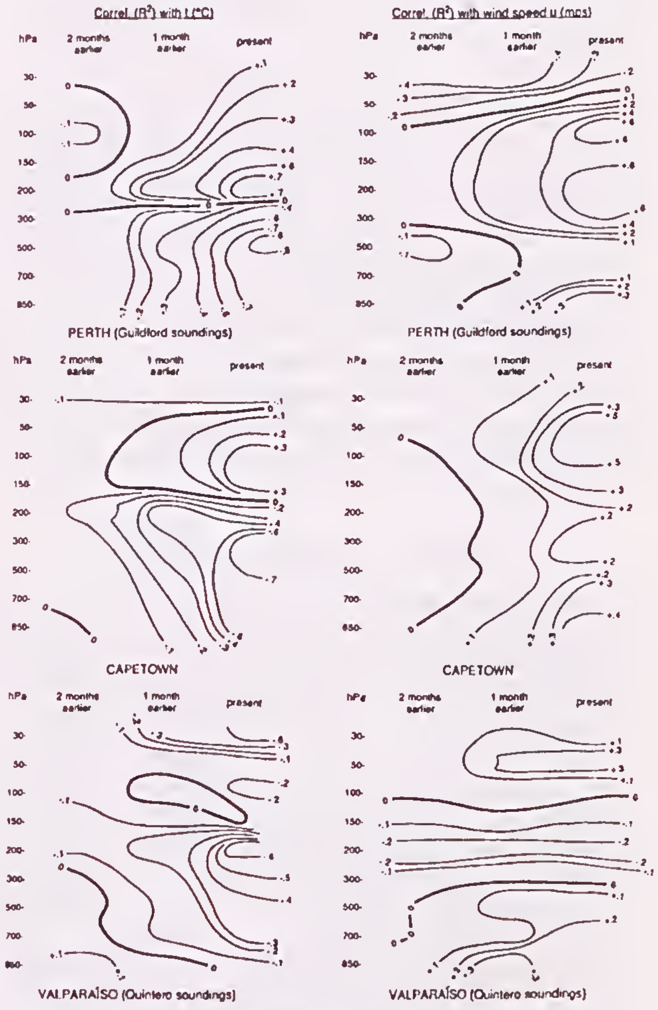

Figure 8 Correlation (R^2) between average monthly rainfall and upper air temperatures (diagrams to the left) and wind speed (diagrams to the right) above Perth, Cape Town and Valparaíso.

At substratospheric heights (200 hPa) above Perth warmer air is closely and positively associated ($R^2 \geq 0.7$) with the rainfall of the same month; this association may be forecast to some extent ($R^2 \geq 0.3$) on the basis of the previous month's 200 hPa temperature. A similar association is much weaker above Cape Town, and non-existent above Valparaíso.

The three regions show a similar but negative relationship (the colder the air above, the greater the rainfall below) at lower levels, but the actual levels of greatest significance differ for each station. Above Perth the closest association ($R^2 \geq 0.8$) is found at 500 hPa; it persists downwards, only slightly reduced, and was also noticeable a month earlier. Above Cape Town

a negative correlation between temperature and underlying rainfall ($R^2 \geq 0.7$) is found from 500 to 300 hPa, a higher and thicker band; it also extends downwards with only a slight loss of closeness ($R^2 \geq 0.6$), and is also noticeable the previous month. Above Valparaíso the correlation is still negative, but conditions are quite different: $R^2 \geq 0.6$ is found at 200 hPa but the closeness of the correlation decreases steadily downwards, to become negligible as it reaches the impenetrable inversion below 850 hPa.

Other, related differences are noticeable in the relationship between upper air winds and rainfall at the surface. Above Perth between 100 and 300 hPa (16 500 and 9500 m) runs an enormous band of strong westerlies (Fig. 3) which are closely and positively associated with the rainfall below ($R^2 \geq 0.6$). Above Cape Town the association is slightly weaker and limited to 50 to 100 hPa. Above Valparaíso the correlation, possibly just significant ($R^2 \geq 0.3$), is restricted to 50 hPa (20 500 m) but begins already in the preceding month; the mechanism of any relationship is worth further investigation. However, no relationship between wind speed and surface rainfall seems to exist at any level below 50 hPa.

Regional thermal differences

World maps of January and July temperatures, from the masterly pioneer maps by van Bebber & Köppen in Hann (1896) to Blüthgen (1966), clearly show regional differences, particularly above offshore waters. In January wedges of air below 20°C reach northward beyond the tropic along the coast of Chile (and along the foot of the Andes) and just off Namibia above the upwelling of cold water from Port Nolloth to Walvis Bay (Höflich 1984). In Chile a core wedge of air below 15°C normally occurs as far as 32°S; there is no counterpart off Namibia. No cool air wedge is shown off Western Australia, on the contrary, surface offshore air above 30° reaches about 20°S (mention of tropical cyclones above). In Angola inland air above 30° just reaches the coast around 18°S; coastal and offshore air off Peru and north Chile stays below 25°C.

Differences are simpler and sharper in July: offshore air below 20°C reaches northward to about 18°S in Western Australia, 8°S off Angola and about 3°S off South America.

In general, maximum and minimum screen temperatures are 6° or 7°C higher at Cape Leveque (16°24'S, Western Australia) than at Mossamedes (15°12'S, Angola) and 7° to 9° higher than at San Juan (15°22'S, Peru), as may be expected from the differences in the adjoining ocean surface temperatures. At Exmouth (24°49'S, Western Australia) mean maximum summer temperatures rise over 16°C above those at Swakopmund (22°41'S, Namibia) and 12° above those at Antofagasta (23°26'S, Chile), but by winter both are reduced to some 4°C. Summer minima are about 6° higher at Exmouth than at Antofagasta, where in turn they are some 2° higher than at Swakopmund. Similar differences are found in winter minima.

Further south, Perth summer maxima are only some 3° above those at Cape Town, but about 8° above those at Valparaíso; summer minima are 2° higher than Cape Town's and over 5° higher than Valparaíso's. In winter travelling anticyclones bring frequent, if transient, inversions over Perth, reducing the differences from the permanent inversions of southwest Africa and Chile. Winter maxima at Perth and Cape Town are very similar, and those at Valparaíso only 2° lower. Winter minima are similar at Perth and Cape Town, and about 1° lower at Valparaíso.

In these regions water masses (and very maritime air) can hold the mean daily range at 5 to 7°C, land masses (and very continental air) can send it soaring to 15 or 18°C. Air circulation therefore determines the season or the month when the greatest or smallest range occurs. Thus at Cape Leveque the narrowest range occurs during the strongest onshore air flow in January-February and the widest one during the anticyclonic offshore flow in July-August, whereas at Vlaming Head the narrowest one comes in June (northwesterly epitropical disturbances and extreme reach of southwesterly mid-latitude fronts) and the widest one in September and also in November-December (probably due to phases in the transit of anticyclones). Loewe (1948) showed that in Australia wider diurnal ranges of temperature as well as higher interdiurnal variability of temperature occur during the drier seasons, *ie* in winter north of the tropic and in summer south of it. On the other hand in western Namibia and South Africa the greater variability occurs in winter and early spring, when the hot dry berg winds descend from the plateau often enough to raise daily maximum temperatures. "In the Namib Desert... the mean monthly temperatures vary little but daily temperatures vary widely and relatively unpredictably..." (Seely 1989).

The influences of cool ocean currents, continental geometry and landforms combine in producing another clear regional differentiation: in tropical Western Australia the month with the greatest mean daily range of temperature, 10 to 15°C, progresses gradually from July at Cape Leveque to October beyond Onslow. In the other regions there is no regular time sequence and the range remains smaller: 10°C in May at Mossamedes, 9.5° in April at Lima and 7.8° in January to March at Arica.

Oceanic influences and onshore air flow combine in giving the southern reaches of all three regions mean daily ranges of 5 or 6°C in June-July, but only along the South American coast where the flow of cool water along the shore is at its strongest does this pattern continue very far towards the equator. On the southwest African coast, where local cool water upwelling is very effective and the cool current is weaker, the months with the narrowest range vary with each station; in Western Australia the time remains unchanged as far as Shark Bay but daily ranges below

6°C are only found on islands, thus confirming the fact that plain oceanic influence is the prime factor in holding thermal ranges small.

The delayed annual thermal maximum in March (in April for mean daily maxima) which occurs around Broome in Western Australia, is also found at Mossamedes in Angola, and is probably due to the time of the second transit of the zenithal sun, the position of travelling anticyclones, and the end of the rainy season. On the Peruvian and Chilean coast the warmest time is more diffuse, probably because of the strong ocean current along the shore, but a faint maximum is usually found in February, as is normal and more definite further south in all three regions.

Conclusions

Evidence so far does not clearly prove any effect of the Leeuwin Current on coastal climates, partly because of deficiencies in the available records of the pairs Abrolhos-Geraldton and Rottnest-Fremantle. At the ocean-air interface, higher temperatures and levels of humidity may be noticed physiologically. As a stream, the Leeuwin Current is only about 30 km wide (Godfrey & Ridgway 1985), although some of its eddies may reach much further to the seaward. Mean minimum temperatures are higher at Rottnest Island than at Fremantle by 1°C in March, 1.4° in April, 1.8° in May: the April-May rise may be partly due to the arrival of warmer water. This suggestion may be supported by the fact that 9 am relative humidity, relatively stable, shows its greatest monthly increase from March to April: 8% at Rottnest, 16% at Fremantle and 9% at Perth, but on the other hand these changes are even more conspicuous further inland, where no significant influence of the Leeuwin Current could be postulated. Karelsky (1961), having defined 'cyclonicity' as the number of cyclonic centres in a particular area during the month concerned, shows an average cyclonicity of 0.6 in March, 1.3 in April, 1.5 in May and 1.9 in June between 30 and 35°S and 110 and 115°E. On the other hand, most rain is brought to south-western Australia by mid-latitude fronts linked with mid-latitude depressions which form over the southern Indian Ocean south of 45°S and west of 75° or 80°E. A count for 1988-1990 shows rain brought to Perth by nearly 100 weather systems a year, some 84 of them meridional fronts formed far to the south-west and crossing over Perth or further south, but including also a dozen 'subtropical' lows formed hundreds of kilometres due west of Perth. The monthly count of rain-bearing fronts agrees with the average of 9.5 fronts (including non-rain-bearing ones) in February and 14 in August shown by Gorshkov *et al.* (1974). Some rain was brought by coastal troughs and by two tropical cyclones. Cloud formations were already conspicuous in satellite images days before they reached the vicinity of the Leeuwin Current. It is possible that some 'subtropical' lows (more frequent in the autumn) and some troughs, slow-travelling or even briefly stationary, could gather additional vapour from the Leeuwin Current, but their formation and main moisture loading took place hundreds of kilometres away.

The most significant and economically important inter-regional climatic differences, particularly in the amount of rain received, are due to the absence of colder water near the Western Australian shore, not to the presence of warmer water: Gorshkov *et al.* (1974) show an average of 14 fronts reaching the coast near Perth in August, against 4 reaching Chile at the same latitude. As to nor'westerly origin of epitropical storms or cloud bands, the water vapour generated by 2.5 million km^2 of warmer water in the Arafura-Cocos region far outweighs what can be generated by the 25 000 km^2 or so of the Leeuwin Current, even when its surface is greatly increased by meanders, swirls and gyres. Air transiting across the current may be made more unstable, but most of the winter thunderstorms seem to be due to the sudden uplift of the fast windstream by the Darling Scarp (Gentilli 1979b).

Immediately above the 'climatic cuticle' affected by the Leeuwin Current is likely to be spreading the mild cooling effect of the much broader West Australian Current, carried by the peripheral winds of the Indian Ocean anticyclone, and partly showing cyclonic divergence long before it meets the western margin of the Leeuwin Current.

In principle, it seems desirable to establish regular climatic observations at the Abrolhos and to extend the scope of the Rottnest ones, particularly in the afternoons. It should also be recommended that detailed studies of sea breezes, land breezes and southerly coastal wind be supported as long-term research projects.

Evidence of contemporary climatic fluctuations should be monitored regularly. Gentilli (1952b, 1971) showed definite patterns (decrease in the Kimberleys, increase in the South-West) for the period 1881-1940. Pittock (1975) found a reversal of this trend after 1941. Vogel's (1988) research seems to show that in 160 years of Cape Town records there is no indication of climatic change, but his graphs reveal definite and fairly regular fluctuations of floods and droughts. Perhaps there is a need for some well-publicised agreement on definitions of climatic singularities, variations, periodicities and fluctuations, and long-term climatic changes, while trying to avoid the stereotyped rigidity that made the concept of 'climatic normal' almost meaningless to research.

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Eastern boundary currents of the southern hemisphere

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Abstract

Traditional atlases show ocean currents forming anti-clockwise gyres in each of the three southern hemisphere oceans, with northwards currents along the west coasts of the continents (the so-called Eastern Boundary Currents). Associated with the equatorwards currents and winds, cool upwelled water is found along the west coasts of southern Africa and South America. However, sea temperature charts reveal that there is in fact a southwards flow off Western Australia, and, despite net equatorwards winds which favour upwelling, there is no large-scale upwelling off this coast.

In this paper, the oceanic circulation in each of the Humboldt (Peru/Chile), Benguela (southern Africa) and Leeuwin (Western Australia) current systems is reviewed. Seasonal sea temperature patterns at the same latitudes clearly show the different thermal regimes operating, with important consequences for the marine biota.

The main features of the Leeuwin Current system are summarised, with emphasis on the mesoscale (10's to 100's km) meander/eddy structure as revealed by satellite imagery. Inter-annual variability in sealevel, which is an indicator of the strength of the Leeuwin Current, is linked with El Niño/ Southern Oscillation (ENSO) phenomena.

Introduction

The West Wind Drift current, driven eastwards around the globe by the strong westerly winds in the Southern Ocean, links the south Indian, Pacific and Atlantic Oceans. In the tropics, the westward-flowing South Equatorial Currents are driven by southeast trade winds. In consequence, there is an anti-clockwise gyre in each of the three southern hemisphere oceans, with relatively intense southwards (or polewards) currents along their western boundaries and weaker equatorwards flows in the eastern boundary current (EBC) regions (Wooster & Reid 1963).

Such is the picture painted by traditional current atlases (see, for example, Tchernia 1980). In the eastern South Atlantic Ocean, there is the equatorwards flow in the Benguela system, while the Humboldt Current system transports cool temperate water northwards off Chile and Peru. Associated with each of these two major current systems is seasonal upwelling of cooler, nutrient-rich subsurface water onto the continental shelf, leading to highly productive waters and rich fisheries.

By contrast, oceanographers have known for decades that the situation off Western Australia is different (Cresswell 1991), with warm water of tropical origin flowing southwards and a distinctive lack of large-scale and persistent upwelling.

This paper briefly reviews the broad-scale circulation off the western coasts of southern Africa and South America, and then focuses on the differences between these two "typical" eastern boundary currents and the anomalous Leeuwin Current. For further information on EBCs in general, the reader is referred to Wooster & Reid (1963) and Neshyba *et al.* (1989).

Large-scale oceanography

The difference between the three southern hemisphere EBCs is effectively illustrated by the mean sea surface temperature (SST) charts for summer and winter (Figs. 1 and 2 respectively).

The northwards deflection of the surface isotherms off Chile and Namibia indicate both the equatorwards flow of cool water from the south and the upwelling of cold subsurface water. Upwelling in both areas is most intense during the summer months, shown by the closed isotherms along the Peru coast between the equator and 15°S, and between 20 and 35°S off southern Africa (Fig. 1). In winter, the westwards extension of the isotherms along the equator reflects the flow in the South Equatorial Current systems (Fig. 2).

Off Western Australia, by contrast, there is a poleward deflection of the isotherms in both seasons (Figs. 1, 2) indicating the southwards advection of warm water, and there is no evidence of upwelling.

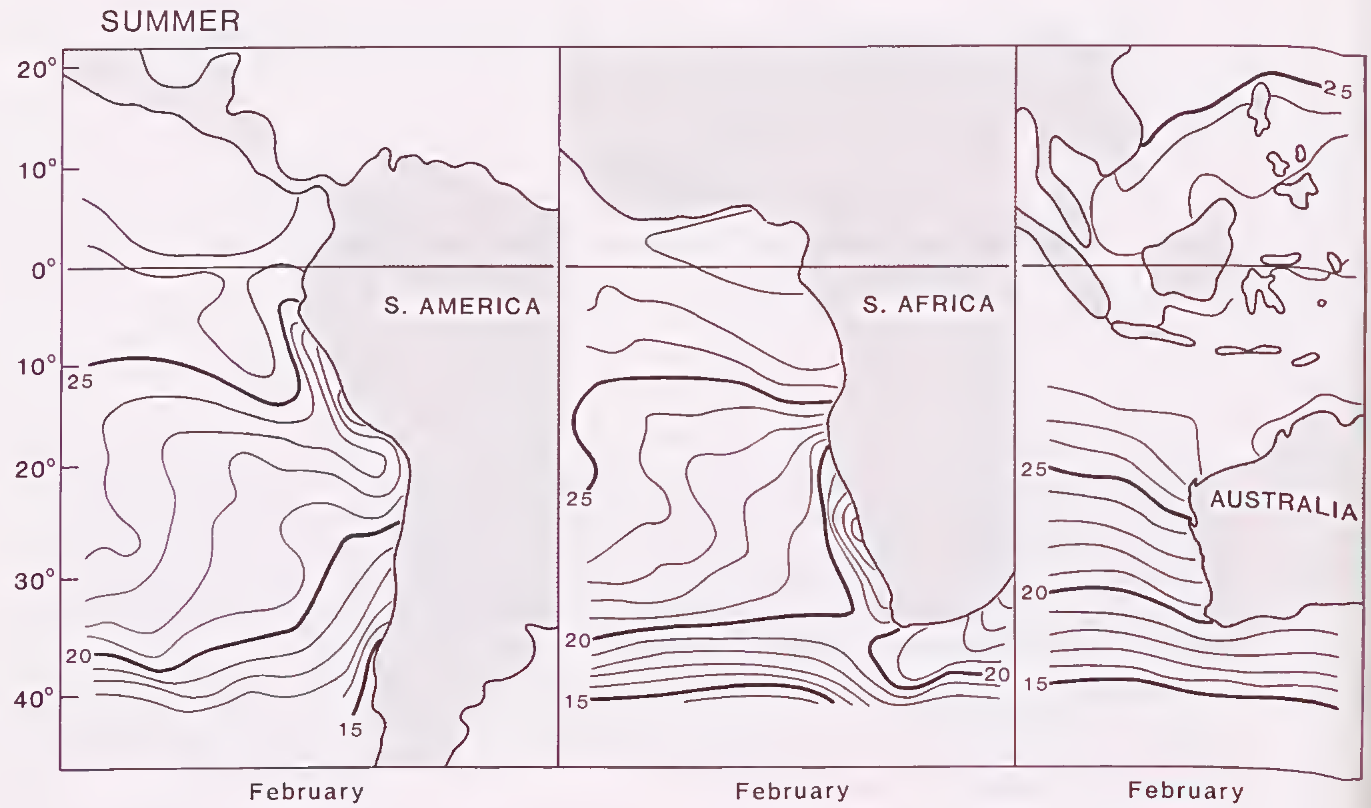

Figure 1 Summer (February) sea-surface temperature charts off the western coasts of South America, southern Africa and Australia (after Reynolds 1982).

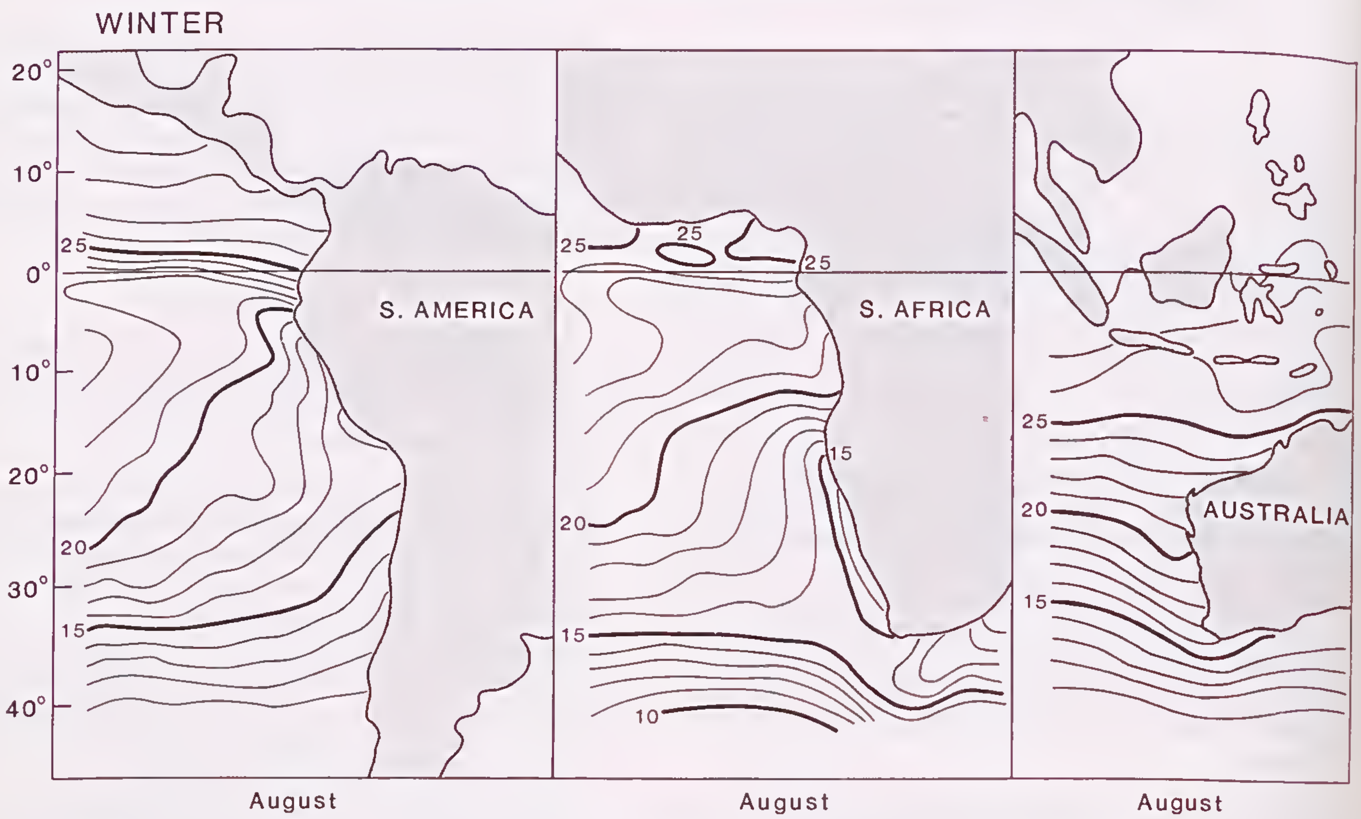

Figure 2 Winter (August) sea-surface temperature charts off the western coasts of South America, southern Africa and Australia (after Reynolds 1982).

Gentilli (1972) illustrated the different thermal regimes in the three areas using SST data derived from ocean atlases. More recent information using the Combined Ocean/Atmosphere Data Set (COADS) enables the zonal surface temperature to be examined on a monthly basis, and again the appreciable differences between the three EBC regions is apparent (Fig. 3; Table 1). In the three areas, the SST at 10 degrees of longitude (about 1000 km) offshore is not appreciably different: about 21°C in summer and 16°C in winter. Off Africa and South America, SST falls by about 3°C towards the coast as a result of the cool northwards flow and the upwelling. On approaching the Australian coast, however, SST rises by 1.5°C in February, and 3.2°C in August (when the Leeuwin Current is flowing strongly). Indeed, the waters near Western Australia are warmer in winter than those near Namibia and Chile in summer.

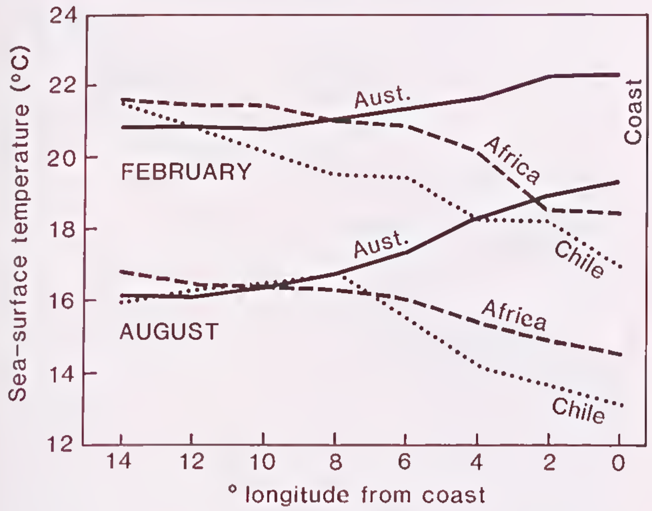

Figure 3 Gross surface thermal structure at 31°S off Western Australia, southern Africa and Chile, derived from COADS monthly data in 2 degree squares.

Table 1

Comparison of summer (February) and winter (August) SST's (°C) at latitude 31°S for the three EBC areas, derived from COADS.

EBC region	February	August
Benguela	18.4	14.5
Humboldt	17.0	13.0
Leeuwin	22.3	19.2

The subsurface structure is also grossly different. Godfrey & Ridgway (1985) have shown that the isotherms off Western Australia deflect downwards towards the continental slope, indicative of the southwards current, whereas off the other two southern hemisphere west coasts there is a strong upward deflection associated both with the northward current and the upwelling.

Primary production (Fig. 4, from FAO 1981) is strong both off Namibia, where production averages over 500 mg carbon $m^{-2} d^{-1}$ in the upwelling region, and off Peru, reaching 500 mg carbon $m^{-2} d^{-1}$ in an isolated patch but generally in the range 250 to 500 mg carbon $m^{-2} d^{-1}$. In west Australian waters, primary productivity is generally less than half the above values.

The abundance of zooplankton mirrors the geographical distribution of phytoplankton (Fig. 5). The Leeuwin Current is again seen to have a much lower biomass than the other two areas, but it is worth noting that there is still some coastal enrichment despite downwelling.

The Benguela system

The ocean circulation off the west coast of southern Africa has been described in some detail by Shannon (1985), who proposed a conceptual model of the Benguela system – Fig. 6 is a simplified version of the main features of the circulation. There is a broad (order 200 km wide, Nelson & Hutchings 1983) northwards drift of cool surface waters beyond the shelf with speeds of 10 to 30 cm s^{-1} (the classical Benguela Current), forming the eastern branch of the South Atlantic anticyclonic gyre. The volume flow in the Benguela Current is estimated to be between 10 and 16 Sv (1 Sv = $10^6 m^3 s^{-1}$; Shannon 1985).

A shelf-edge jet, first investigated by Bang & Andrews (1974), has been found to extend from south of Cape Town to a point near 31°S where it turns westward. This is a permanent baroclinic jet which has a width of some 10 km, extends down to 120 m and attains core velocities of 60 cm s^{-1} where the shelf is steepest.

Satellite-tracked buoys released off Cape Town during summer moved northwestwards and suggested that topographical steering plays an important role in the trajectory of the Current (Nelson & Hutchings 1983). Current speeds deduced from the buoy tracks were up to 35 cm s^{-1} in the shelf-edge jets. A branch of the Benguela Current continues to penetrate northwards along the coast as far as about 12°S, but the main body of water diverges from the coast and joins a warm saline flow from the north (the Angola Current) in moving westwards between latitudes 15 and 20°S. There is a frontal (convergence) zone between the cool waters of the Benguela system and the tropical/equatorial water of the Angola Current. The front varies seasonally in position and strength but generally lies between about 15 and 17°S and has a surface thermal gradient of about 4°C per 1° latitude (Shannon *et al.* 1987).

Further offshore between 0 and 5°E longitude, there appears to be a northwards meandering jet over the Walvis Ridge.

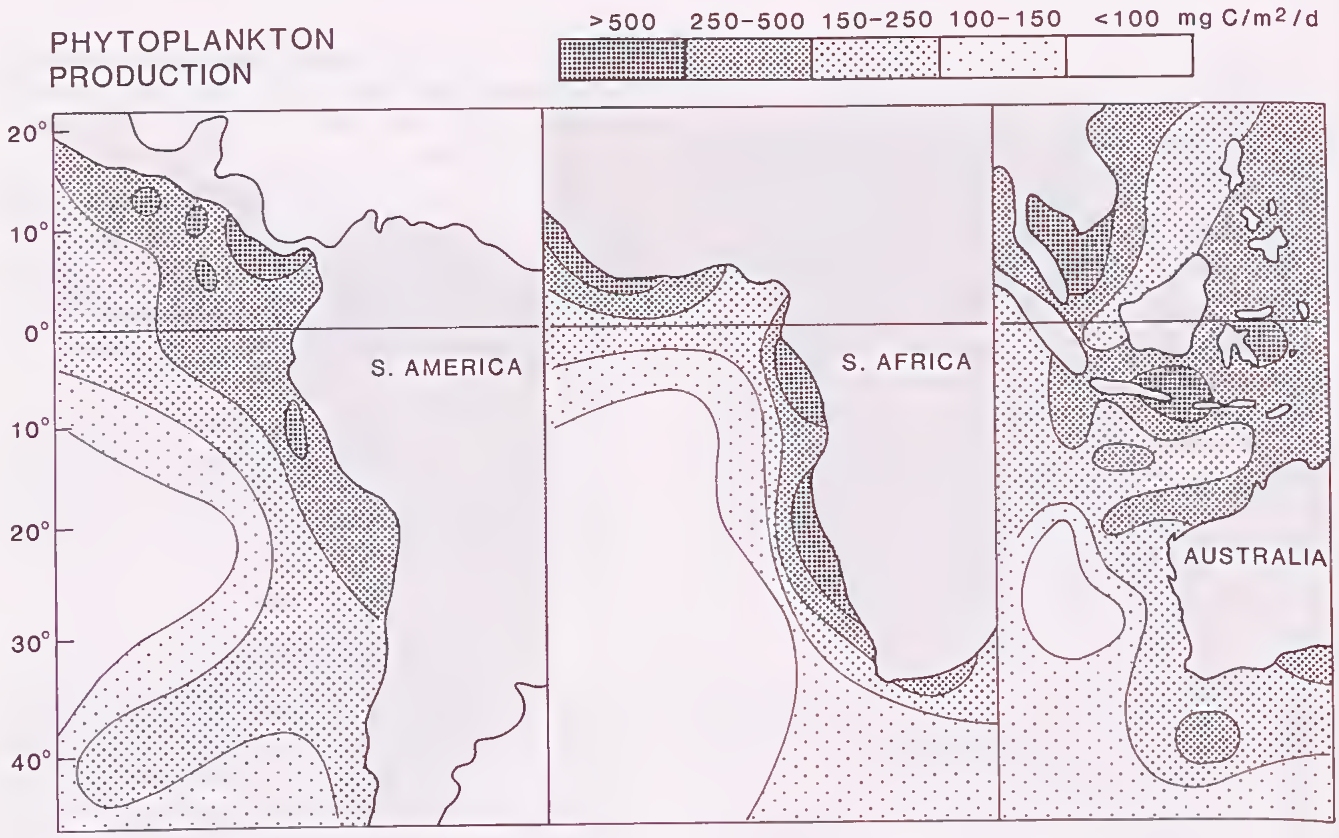

Figure 4 Phytoplankton production (mg C m^{-2} d^{-1}) off the western coasts of South America, southern Africa and Australia (after FAO 1981).

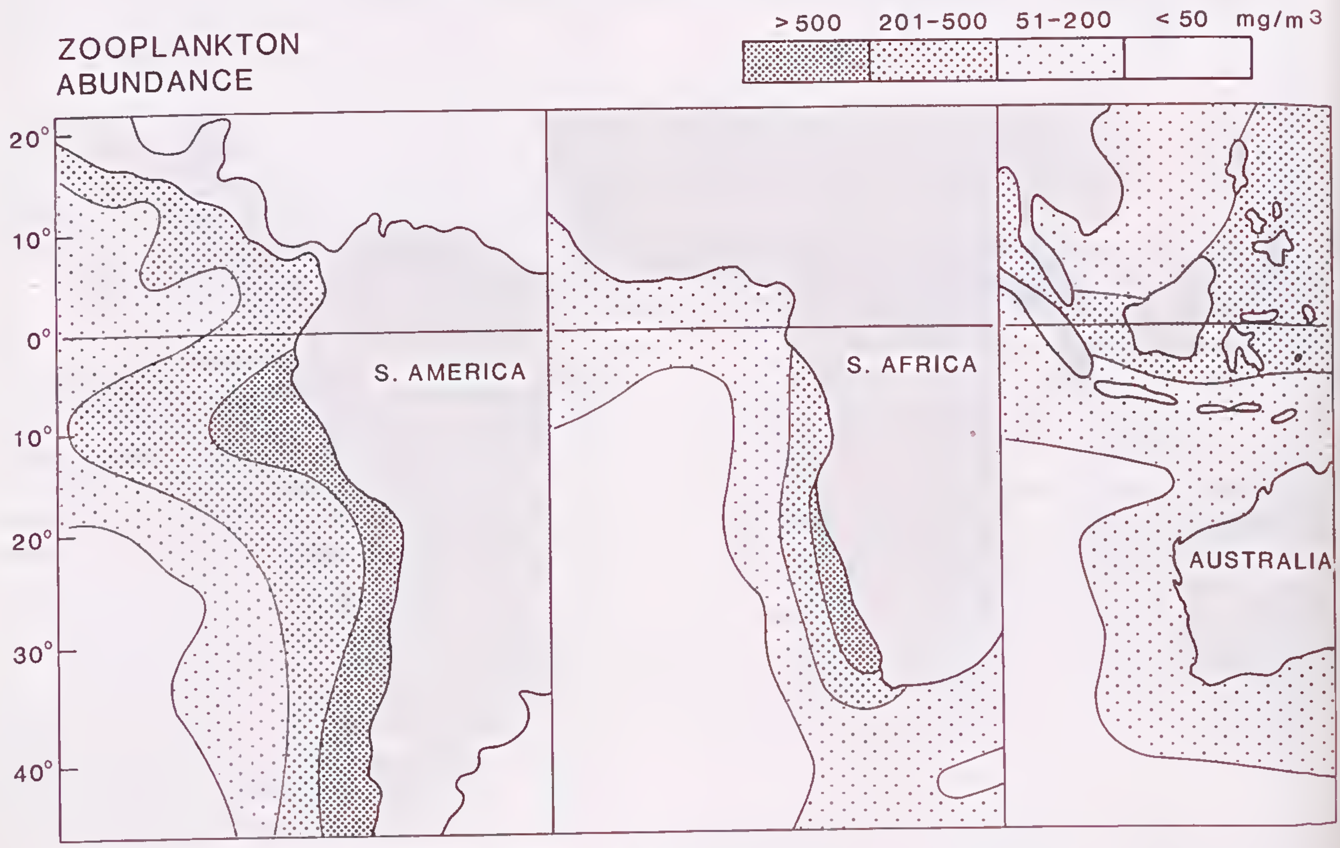

Figure 5 Zooplankton abundance (mg m^{-3}) off the western coasts of South America, southern Africa and Australia (after FAO 1981).

Below the surface there is a deeper poleward "compensation" countercurrent which reaches as far south as Luderitz at 27°S (Hart & Currie 1960); it is generally characterised by low oxygen content. Nelson (1989) has shown that there is in fact an ambient poleward undercurrent of some 5 cm s^{-1} flowing along the whole shelf, shelf-edge and slope regions. This current is modulated by barotropic coastal-trapped waves with two to five day periodicity. On the inner shelf, the flow attains speeds of 40 cm s^{-1} over short periods during the poleward phase. The destiny of the shallower poleward flow in the Cape Peninsula area, where the shelf is very narrow and the coastline turns westward, is unknown, but at least a part is known to follow the coast onto the Agulhas Bank. A part may retroflect into the shelf-edge jet.

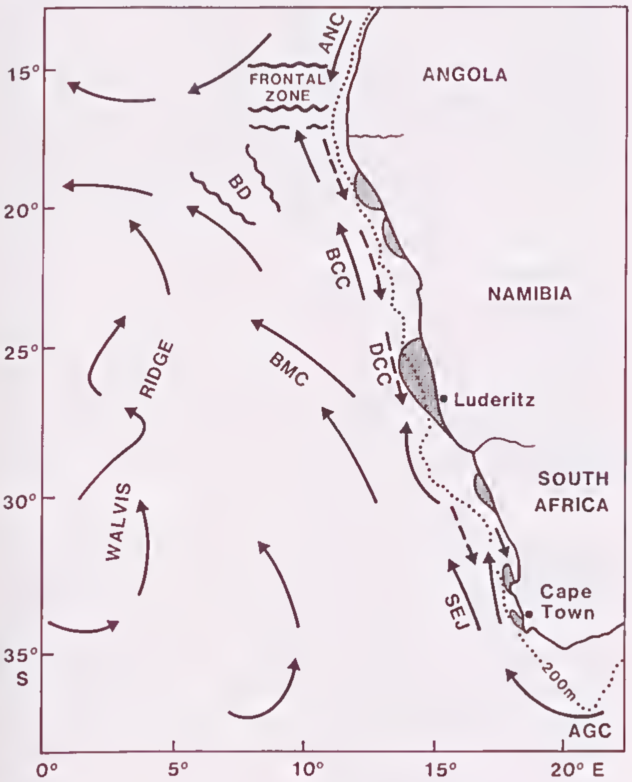

Figure 6 Conceptual model of the Benguela system, simplified from Shannon (1985). AGC = Agulhas Current, ANC = Angola Current, BCC = Benguela Coastal Current, BD = Benguela Divergence, BMC = Benguela Main Current, DCC = Deep Compensation Current, SEJ = Shelf-edge jet. Regions of locally enhanced upwelling are shaded. Solid arrows are surface currents, dashed are subsurface. The dotted line shows the 200 m contour.

The prevailing winds are from the south, and hence upwelling-favourable, although both seasonal and alongshore variations in wind stress occur. There are in fact two distinct regimes in the upwelling system, separated at about 31°S: the southerly region experiences a clear seasonal wind-driven upwelling pattern (upwelling is strongest in spring and summer when the northwards wind stress is strongest), whereas north of 31°S the upwelling is more perennial. The upwelling regime consists of a series of localised upwelling cells along the 1700 km of coastline between 20 and 35°S (the shaded near-coastal features in Fig. 6).

The Humboldt system

The Humboldt (or Peru-Chile) current system off South America is a classical eastern boundary upwelling region, exhibiting the characteristics of equatorward surface flows associated with wind-driven coastal upwelling, high biological productivity and rich fisheries. The upwelling is most pronounced off the Peru coast (4 to 18°S), which has, as a result, been studied in more detail than the Chilean region, and less information is available for the current regime south of 25°S. This review of the circulation in the upper few hundred metres is taken largely from Gunther (1936), Wyrtki (1963, 1966), Zuta (1988) and Codispoti *et al.* (1989). Authors differ in their conclusions on some aspects (partly a result of the different seasons in which surveys have been undertaken), but this synthesis attempts to summarise the main features of the circulation.

Surface currents off this coast are generally towards the north (Fig. 7) as described earlier. The Peru Oceanic Current (POC), which forms the eastern limb of the anti-cyclonic circulation of the South Pacific Ocean, extends to about 700 m depth. North of about 20°S, it diverges from the coast, flowing westwards south of 10°S and entraining or merging with water from the Peru Countercurrent (PCCC) and the Equatorial Countercurrent (SECC) as it returns westwards to form the South Equatorial Current (SEC). Wyrtki (1963) places the eastern limit of the POC off central Peru at about longitude 82°W. It consists largely of Subtropical Surface Water from the South Pacific Ocean, transporting about 8 Sv at 24°S increasing to 14 Sv as it heads westward (Wyrtki 1966).

Nearer the coast lies the northwards Peru Coastal Current (PCC), which is shallower (<200 m) than the POC. Its southern and northern limits vary seasonally, but lie approximately between about 33 & 40°S and 5 & 10°S respectively (Gunther 1936; Wyrtki 1963). Wyrtki (1963) considers that it lies east of about 78°W off central Peru; it transports about 6 Sv.

Between the two north-flowing currents, the Peru Countercurrent (PCCC) carries warm equatorial subsurface waters southward, commencing at the coast at about 5°S and then flowing almost due south along 80°W. It draws some of its water from the northern extremity of the Peru Coastal Current. It is about 250 km wide and extends down to about 500 m, but its maximum strength is at about 100 m depth. It is not always evident at the surface because of wind-driven surface currents. The PCCC transports about 11 Sv

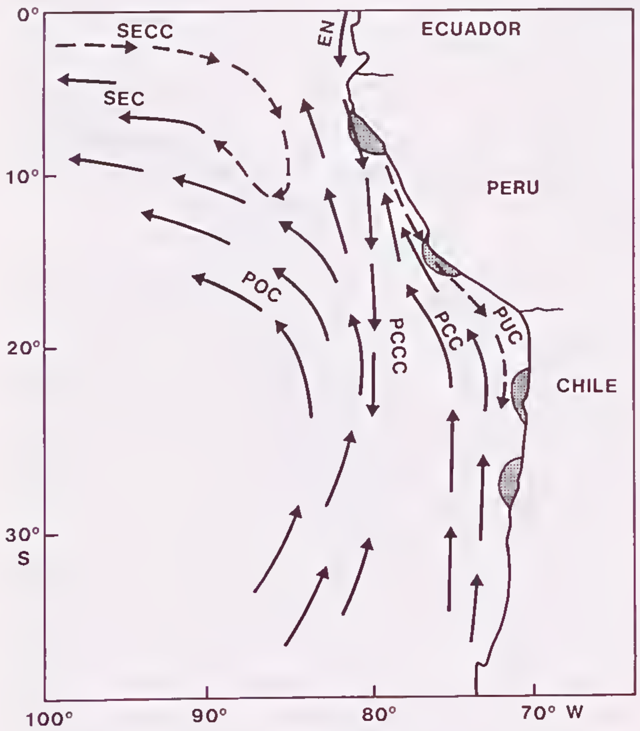

Figure 7 Simplified diagram of the main features of the ocean circulation off western south America, largely after Wyrtki (1966) and Zuta (1988). EN = El Niño Current, PCC = Peru Coastal Current, PCCC = Peru Countercurrent, POC = Peru Oceanic Current, PUC = Peru Undercurrent, SEC = South Equatorial Current, SECC = South Equatorial Countercurrent. Regions of supposedly enhanced upwelling (Gunther 1936) are shaded to illustrate the alongshore variability of upwelling. Solid arrows are surface currents, dashed are subsurface.

southwards at 6°S, and weakens to 6 Sv at 15°S and 2 Sv by the time it reaches 22°S.

Below the surface near the coast, there is the southward-flowing Peru Undercurrent (PUC), which is separate from the Peru Countercurrent further offshore (Wyrtki 1963, Brockman *et al.* 1980, Huyer *et al.* 1991). Poleward undercurrents of this nature, flowing counter to the dominant wind, are persistent and important features of most upwelling regions (Smith 1983). At 15°S, the Peru Undercurrent extends across the shelf under a thin (30 m) equatorward wind-driven surface layer, and down the upper slope to a depth of about 250 m and offshore extent less than 50 km from the shelfbreak. Maximum flow occurs between 50 and 150 m depth; the transport is about 1 Sv at 10°S (Huyer *et al.* 1991). The southern limit of the PUC has been estimated by Silva & Neshyba (1979) to lie at about 48°S.

Brattström & Johanssen (1983) have suggested that there is a Chile Coastal Countercurrent (which flows southwards) and a north-flowing Chile Coastal Current, both inshore of the Peru Undercurrent. These currents, which are present along sections of the Chilean coastline, have not been included in Fig. 7 for clarity.

The South Equatorial Countercurrent (SECC) carries some 11 Sv of low-salinity, warm equatorial surface water into the area from the west, as a surface/subsurface flow between about 4°S and 7°S. It deflects southwards at about 85°W, and then at about 15°S returns westwards and merges with the Peru Oceanic Current (Wyrtki 1963). Wyrtki (1966) has no mention of a countercurrent south of the equator, but shows an eastwards Undercurrent carrying 35 Sv along the equator; some of this returns westwards with the SEC, while the rest runs southward along the shelf as an undercurrent.

There is an intermittent poleward intrusion of warm, low salinity equatorial water down the coast of northern Peru (Murphy 1936), associated with interannual variations in the central and western Pacific. This nutrient-poor water generally manifests itself at about Christmas time, and has the traditional name of "El Niño" (or "the Christ-child"). At intervals of between 2 and 10 years, this intrusion is extensive and devastating, raising the temperature of the water by many degrees, lowering the thermocline and thus adversely affecting the upwelling process. Plankton and fish die and decompose, birds starve or leave the area, and the commercial fishery collapses. Such events are now known as "ENSO events", as the El Niño is in fact merely one manifestation of a chain of global oceanic and atmospheric phenomena associated with the Southern Oscillation, which is a major reversal of the atmospheric pressure fields in the Indian and Pacific Oceans (Quinn *et al.* 1978, Cane 1983).

In some localised regions, upwelling of nutrient-rich waters onto the continental shelf is stronger in autumn and winter (May to September) than in spring/summer (Zuta 1988). Instead of upwelling occurring simultaneously all along the coast, upwelling cells tend to develop with offshore scales of order 10's of kilometres (Smith 1983). Gunther (1936) describes the existence of locally enhanced upwelling cells which appear to be associated with highly variable anticyclonic eddy-like circulations along the coast, as a result of alongshore variations in both topography and wind stress. His observations agreed substantially with those of some earlier investigators, finding stronger upwelling centred at about 28°S, 23°S, 15°S and 7°S (Fig. 7). As pointed out by Wyrtki (1966), however, localised upwelling centres may in fact occur anywhere along the coast. The upwelling zones north of about 12°S are supplied by high salinity, low oxygen water in the poleward countercurrent PUC at depths of order 100 to 150 m; further south, the source of upwelled water is the lower layer of the less saline Peru Coastal Current (Wyrtki 1966). Both of these water masses are drawn up onto the shelf during upwelling events.

The difference in the general location of the strongest upwelling centres between Peru and Namibia

reflects a similar variation in the strength of the offshore Ekman transport.

The Leeuwin system

In contrast with the above two classic EBCs, the Leeuwin Current exhibits many unusual features (Figs. 8,9).

The general anticyclonic flow which must complete the circuit of the southern Indian Ocean to maintain continuity of flow, takes about 3 years to complete the cycle; surface drift cards suggest that the mean current speed is about 17 cm s^{-1} (Shannon *et al.* 1973). In the southeastern region of the Indian Ocean, however, there is a large alongshore pressure gradient between the warm (low-density) equatorial waters and the cool (high-density) Southern Ocean (Thompson 1984 and Godfrey & Ridgway 1985). This meridional gradient, which is much stronger than that in the other corresponding eastern boundary current regions (Fig. 10), induces a net eastwards geostrophic flow from the Indian Ocean towards Australia, and the flow is then deflected down the pressure gradient by the continent to form the Leeuwin Current (Fig. 8).

Godfrey & Weaver (1991) suggest one reason that such a large gradient is found off Western Australia and not off any other eastern ocean boundary has to do with the existence of the open Indonesian passages. These result in vertical temperature profiles off the Northwest Shelf being very similar to those in the (very warm) western equatorial Pacific. The warm water supply leads to a loss of heat to the atmosphere and convective overturn of the water column between about 20 and 36°S, and hence to the unique alongshore pressure gradient of Fig. 10.

A summer feature, named the "West Australian Current" by Andrews (1977), meanders eastwards between latitudes of about 29 and 31°S, and deflects southwards offshore of the Leeuwin Current along the continental margin. This current appears to be a branch of the traditional northwards current of the same name which forms the eastern limb of the south Indian Ocean gyre, and it may perhaps be better to retain the name in its original usage. Andrews' current could be termed the "West Australian Summer Current" (Fig. 9).

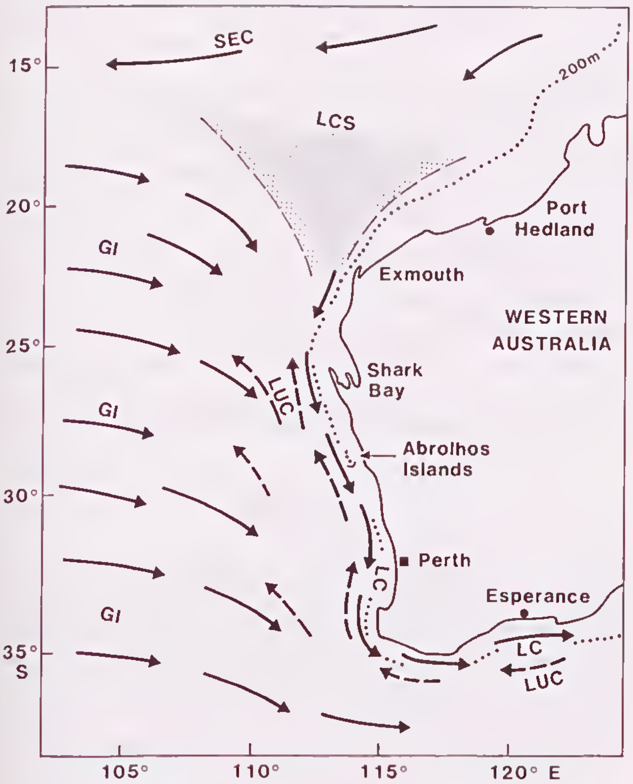

Figure 8 Schematic diagram of the main features of the Leeuwin Current system. GI = geostrophic inflow from the open ocean, LC = Leeuwin Current, LCS = Leeuwin Current source area, LUC = Leeuwin Undercurrent, SEC = South Equatorial Current. Solid arrows are surface currents, dashed are subsurface. The dotted line shows the 200 m contour.

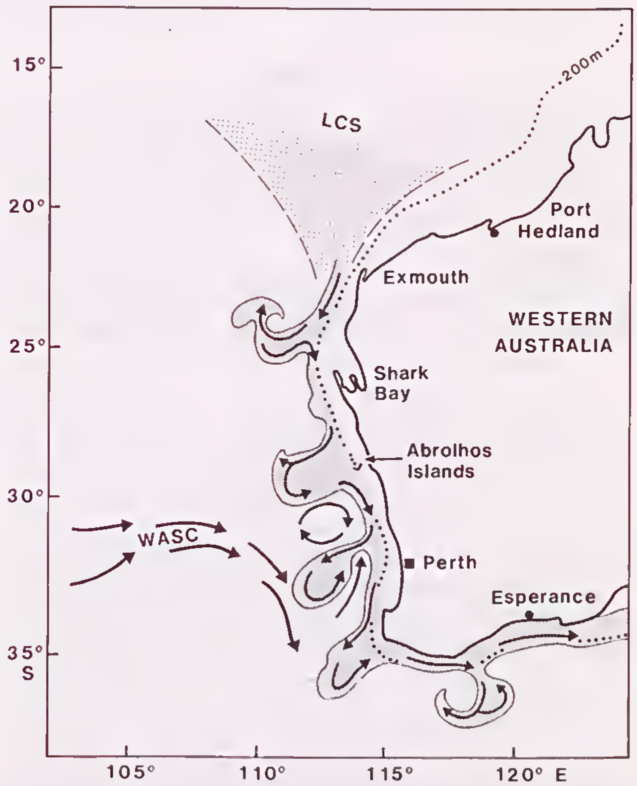

Figure 9 Schematic diagram of mesoscale features of the Leeuwin Current system, derived largely from satellite imagery. The Leeuwin Current itself is shaded, the solid arrows indicating the flow in the warm surface meanders and jets as well as the currents in the cooler offshore waters. WASC = West Australian Summer Current (modified from Andrews 1977). The dotted line shows the 200 m contour.

Despite equatorward (upwelling-favourable) winds (Godfrey & Ridgway 1984), there is no upwelling off Western Australia. This lack of upwelling is clearly illustrated by comparing the vertical structure of the upper water column on the continental shelf at about 32°S with that in the Benguela area (Fig. 11). In the Benguela, surface temperatures just beyond the shelf-break exhibit the expected seasonal pattern, with summer values of about 19°C falling to 15°C in winter. Closer inshore, however, in water depths of 80 to 150 m, the surface temperature is about 14°C in all months with minimal seasonal variation. Just 20 m below the surface, the temperature is about the same as at the surface during winter, but in summer it falls by almost 4°C as a result of the upwelling. There is, therefore, a reversed seasonal pattern below the surface off southern Africa, the water being warmer in winter than in summer (Fig. 11). Off Western Australia, by contrast, temperature measurements in 55 m water depth show that the column is well-mixed in all seasons, with mean summer temperatures of about 22°C falling to 19°C in winter.

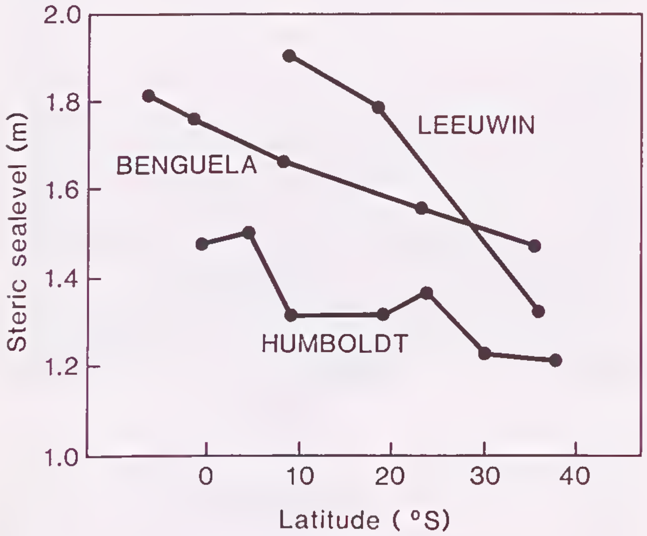

Figure 10 Alongshore sealevel difference on the eastern boundaries of the south Pacific, Indian and Atlantic Oceans (adapted from Godfrey & Ridgway 1985).

Thompson (1984) reported the existence of an equatorward undercurrent a few hundred metres below the Leeuwin Current off Shark Bay. This countercurrent, which transports high-salinity South Indian Central Water northward and offshore (Fig. 8), is also reflected in the geopotential topography of the 300 m surface relative to 1000 m (Wyrtki 1971).

LUCIE

The most comprehensive survey of the Leeuwin Current system to date was undertaken in 1986 and 1987, known as the Leeuwin Current Interdisciplinary Experiment (LUCIE). The following brief review draws from LUCIE papers by Church *et al.* (1989), Weaver & Middleton (1989) and Smith *et al.* (1991), as well as the important papers by Thompson (1984), Godfrey & Ridgway (1985) and Batteen & Rutherford (1990). It will concentrate on features of the Current south of Exmouth (22°S); the "source area" to the north has been dealt with by Church *et al.* (1989) and by Cresswell (1991). It should be pointed out that 1986/87 was an ENSO period, so the Leeuwin Current may not have been "typical" at that time (Pearce & Phillips 1988, Smith *et al.* 1991).

The Leeuwin Current is relatively narrow (200 km in the north, narrowing to 50 to 100 km in the south), and shallow (50 m in the north to 200 m in the south) (Church *et al.* 1989). It flows more strongly during the autumn, winter and early spring months than in summer. Peak current speeds can exceed 1.5 m s^{-1} (or 3 knots).

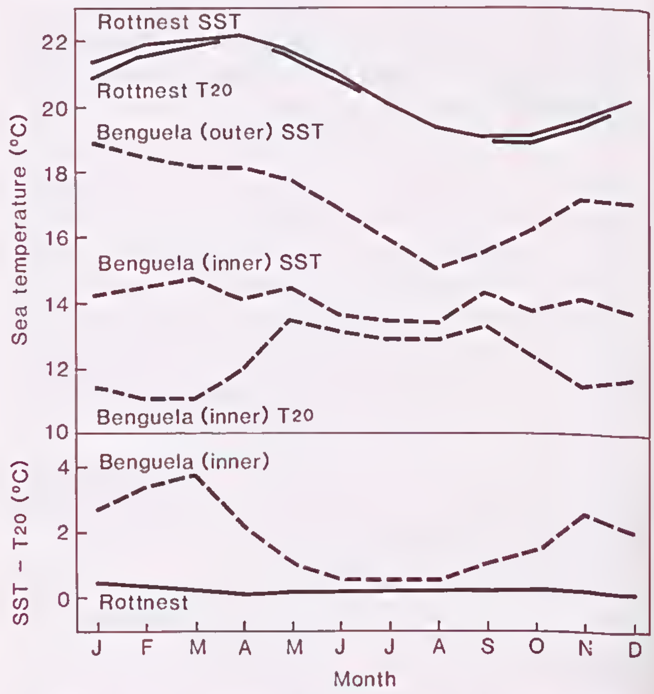

Figure 11 Comparison of the monthly mean thermal structure on the continental shelf at 32°S: Benguela and Leeuwin systems. The Benguela (inner) site was in 100 m water and the outer in 360 m depth (data from Buys 1957). The Leeuwin Current data is from 55m water depth. SST represents sea-surface temperature, T20 is the temperature at 20 m depth. The lower diagram depicts the thermal differential between the water surface and 20 m depth.

LUCIE results indicated that, near the Abrolhos Islands during the spring months, there was a net southward flow of 20 cm s^{-1} in the current core over the upper slope and a northwards undercurrent of 10 cm s^{-1} below about 300 m. In autumn, the southwards jet had strengthened to 55 cm s^{-1}, and the

undercurrent was very much weaker than in spring. By winter, the alongshore flow to the south had moved further offshore but hydrographic measurements showed that it was still flowing very strongly. The flow in the upper 100 m of water just offshore of the shelfbreak near the Islands was remarkably persistent to the south between February and August. The southwards transport in the Current increased from 1.4 Sv in summer to almost 7 Sv in mid-winter.

Along the south coast, the Leeuwin Current was located just beyond the shelf-break (Cresswell & Peterson , unpubl.). A warm offshoot some 50 km wide and 130 m thick was transporting the warm water 200 km southwards into the Southern Ocean, the maximum speed being about 1 m s^{-1}. There was a westward undercurrent at a depth of 400 to 700 m, with a core speed of about 20 cm s^{-1}.

Satellite imagery

The pioneering satellite work of Legeckis & Cresswell (1981) directly confirmed earlier concepts of the southward transport of warm water and the seasonal nature of the Leeuwin Current. NOAA AVHRR (Advanced Very High Resolution Radiometer) satellite images received in Perth have subsequently shown the complex nature of the Leeuwin Current.

Superimposed on the narrow southwards flow of warm, low-salinity tropical water along the shelf-break is a series of wave-like meanders which transport Leeuwin Current water away from and back towards the coast (Fig. 9). Pearce & Griffiths (1991) have shown that the meanders generally develop into cyclonic-anticyclonic eddy pairs: the anticyclonic wing (in particular) grows offshore to a width of order 200 km and may eventually "pinch-off" to form a free-standing eddy. Batteen & Rutherford (1990) have recently modelled the generation of meanders and eddies through both barotropic and baroclinic instability processes.

Between the meanders, the Current tends to flow along the shelf-break and upper slope as a jet-like current towards the south, and cyclonic eddies in the ambient water offshore can be associated with current speeds of over 80 cm s^{-1} (over 1.5 knots). The meanders do not appear to propagate along the coast. Similar structures occur along the south coast (Griffiths & Pearce 1985a); on at least one occasion, a warm eddy drifted southwards into the Southern Ocean (Griffiths & Pearce 1985b).

The western (offshore) boundary of the Leeuwin Current is generally well defined, with a temperature differential of 2 to 5°C between the warm Current water and that offshore, associated with a strong cyclonic shear zone (Cresswell & Golding 1980). The inshore boundary is less clearly defined as the thermal gradient is weaker. Nevertheless, small-scale (order 20 km) billows indicate zones of current shear and active exchange of water between the Current and the shelf water (Pearce & Griffiths 1991).

Interannual variability

Pearce & Phillips (1988) have demonstrated that annual mean coastal sealevels (which may be used as one indicator of the strength of the Leeuwin Current) fluctuate with ENSO (El Niño/Southern Oscillation) events. During ENSO years, relatively low coastal sealevels imply a weaker Leeuwin Current, and conversely, in anti-ENSO years, higher mean sealevels indicate stronger southwards flow. Pattiaratchi & Buchan (1991) have extended the analysis to show that coastal sealevels off Western Australia have been related to ENSO events since the turn of the century.

Temperature and salinity measurements along the outer shelf off Perth confirm that, during ENSO periods, the water along the outer shelf is relatively cooler and more saline than in anti-ENSO years, indicative of less tropical water being advected southwards by the Current (Pearce & Phillips 1988). Pearce & Phillips (1988) and Phillips *et al.* (1991) discuss the implications of this interannual fluctuation in flow for larval recruitment of the western rock lobster.

Conclusions

The Leeuwin Current has been shown to be quite different from the corresponding EBCs of the other two southern hemisphere oceans. Off Namibia and the Peru-Chile region there are cool northward currents, and the upwelling of nutrient-rich water results in highly productive waters on the continental shelf. Off Western Australia, by contrast, the Leeuwin Current transports warm tropical water southwards and (despite upwelling-favourable winds) there is no upwelling.

The difference seems to be largely associated with the flow of warm Pacific Ocean water through the Indonesian Archipelago, leading to a much stronger meridional pressure gradient off Western Australia than exists off Africa or South America.

Poleward under/countercurrents exist off southern Africa and the Peru-Chile region, but they are comparatively weak in comparison with the Leeuwin Current. Instead, there is an equatorwards undercurrent beneath the Leeuwin Current – this is not found along any other eastern boundary.

Interannual variability of coastal sealevels (which may be used as an indicator of the strength of the alongshore flow) is linked with ENSO events, such that the Leeuwin Current is relatively weak in ENSO years and stronger during anti-ENSO periods.

Acknowledgements I am indebted to Dr Vere Shannon and Dr Jane Huyer for helpful suggestions on the Benguela and Humboldt systems respectively, and to Dr George Cresswell, Dr Stuart Godfrey and Dr Chari Pattiaratchi for general comments. Richard Litchfield and Bert de Boer carried out the COADS programming. Ms Liz Jefferson drew the diagrams.

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The Abrolhos carbonate platforms: geological evolution and Leeuwin Current activity

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Abstract

The Houtman Abrolhos reefs comprise three carbonate platforms situated between latitudes 28° and 29.5°S on the western continental margin of Australia, close to the present southerly limit for coral growth. The geomorphology of the platforms and their low islands varies from atoll-like in the south to less regular forms in the north. "Blue-hole" terrains are conspicuous elements of the eastern parts of the platforms. Lagoon sand sheets are dominated by corals and calcareous red algae, in contrast to shelf sediments which are composed of bryozoans, calcareous red algae, molluscs and foraminifers. The coral reefs of the Abrolhos platforms have a probable maximum thickness of 130m, and postdate open carbonate shelves of Paleocene to Upper Eocene age. The growth history of the Abrolhos over the last few hundred thousand years is closely linked to global sealevel fluctuations. Late Quaternary stratigraphy exposed in platform islands is dominated by coral-algal framestone/bindstone and rudstone, for which preliminary dates suggest a Last Interglacial age (*ca* 125 ka BP). Late Holocene coral reef development is largely restricted to leeward reef slopes, walls of "blue-holes", and leeward, more easterly surfaces of platforms. The persistence of reef growth during the Quaternary is linked to the presence of the Leeuwin Current, which probably only came into existence during the Early to Middle Pleistocene. The widespread development of Last Interglacial coral reefs at the Abrolhos and along the western continental margin to latitudes as far south as 34.5°S, and faunal data, support a period of vigorous Leeuwin Current activity. The known distribution of Holocene coral reefs is far more limited, both in areal extent at the Abrolhos, and latitudinally. These differences are probably largely due to fluctuations in Leeuwin Current activity.

Introduction

The Houtman Abrolhos (Fig. 1) are a series of shelf-edge coral reefs which form the southernmost coral reef complex in the Indian Ocean. The Abrolhos reef complex is unique in its location off a western continental margin. It is well known that a general explanation for global reef distribution is sea surface temperature (*eg* Stoddart 1969, Levinton 1982). The limits to normal coral growth are 17-18°C and 33-34°C. Coral growth along west coasts of continents is generally limited by the presence of a cold boundary current which lowers sea surface temperatures, for at least part of the year, below the limit of coral growth; examples of these are the California, Humboldt and Benguela Currents. The presence of the Leeuwin Current along the western margin of Australia results in sea surface temperatures which allow the development of major reef complexes as far south as 29.5°S, the southern limit of the Abrolhos.

This paper describes the geomorphology, geology and Late Quaternary history of the Abrolhos coral reefs and carbonate platforms, and, as far as this is possible with present knowledge, examines the influence of the Leeuwin Current on the growth history of the reefs.

Geomorphological and geological characteristics and sediments

The Abrolhos carbonate platforms are at the northern end of the Rottnest Shelf, a narrow, open carbonate shelf which lies along the quiescent rifted margin of southwest Australia (Veevers 1974, Smith & Cowley 1987, Collins 1988). The Abrolhos are located within the Abrolhos Sub-basin, a part of the Perth Basin. Little previous work has been undertaken on the geology of the reef complex. Teichert (1947) and Fairbridge (1948) have provided important introductions to the geology and geomorphology of the reef complex. More recently France (1985) studied the Holocene geology of the Pelsaert Group.

The Abrolhos reef complex is located at the margin of the shelf and water depth increases steeply to the west (Fig.1). A number of terraces are evident along the shelf edge extending to a depth of 115 m (Harris 1989

unpublished data). The emergent parts of the reef are in three island groups (Fig. 1). Deep channels reaching depths of *ca* 40 m separate the central Easter Group

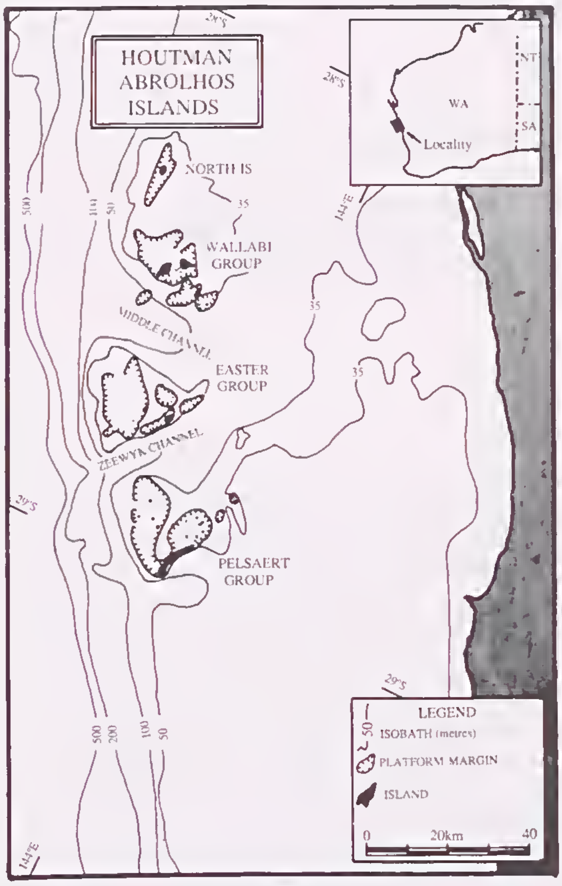

Figure 1 Location map of Houtman Abrolhos Islands and carbonate platforms.

from the adjacent northern and southern island groups. The islands are generally low in elevation, and often amount to little more than small tabular platforms, rising some 3 - 5 m above present sealevel. The exception is provided by the Wallabi Group and North Island where Late Quaternary dune units result in elevations of up to 15 m.

The three island groups differ significantly in their overall geomorphological expression. The Pelsaert Group is approximately triangular in shape, with a strongly defined bounding reef margin rimming the lagoon, except along the poorly defined northern rim (Fig. 1). The Easter Group has a more complex and less "enclosed" geomorphological expression. It consists of a series of arcuate island chains, separated by deep channels ("passages", *eg* Easter Passage) and located leeward of the western reef margin and associated lagoon. The Wallabi Group is dominated by the two large islands, West and East Wallabi, and generally lacks the geomorphological organization of the other island groups. Well developed lagoon sandsheets are prominent elements of the Pelsaert and Easter Groups. "Blue-hole" terrains are a conspicuous element of the geomorphology of the eastern parts of the island groups, but are absent from the western parts. In other parts of the world "blue-holes" have been interpreted as having a solutional karst - doline origin (see the summary discussion of Purdy 1974). However, in the Abrolhos the precise origin of "blue-hole" terrain is unknown, and depositional and lithofacies factors may have controlled "blue-hole" development. There is a marked contrast between western and eastern substrates of the platforms. Well lithified coralline algal-coral lithofacies of the west differ sharply from poorly lithified branching-coral framestones and rudstones of the east. The latter are at least 25 m thick beneath "blue-hole" terrain in the Easter Group, and these low-strength, vuggy limestones are potentially far more vulnerable to collapse and/or solution processes.

Lithofacies characteristics and distribution

Quaternary sediments of the Abrolhos platforms and adjacent shelf are both reef framework and bindstone facies, generated by corals and encrusting coralline algae, and fragmental facies, which comprise shelf and platform sand sheets and rudstone accumulations. Coral growth is generally poor on the windward reef slopes where bindstone lithofacies dominate. Lagoon patch reefs are prominent elements and are especially evident in the Pelsaert Group. The leeward reef slopes and associated deep channels support an extensive coral cover.

Holocene bindstones generated by encrusting red algae form veneers over intertidal substrates along reef crests, overlying rocky substrates, and in shallow lagoon areas, encrusting either rock substrates or coral framestones. These veneers are usually <20 cm thick. Holocene coral framestones are present as thin veneers or reef accumulations. Lagoon substrates and walls of "blue-holes" have well developed framework communities. France (1985) has suggested a potential maximum thickness of 5 m for framework facies, but no subsurface data are yet available to substantiate this claim. Emergent rudstone facies, forming storm-beach ridge sequences, are prominent elements of the geomorphology of the islands of the leeward regions of the reefs.

The spatial distribution and character of these lithofacies is well reflected in the make-up and stratigraphy of the islands (Fig. 2). In general, the central portions of the platforms are dominated by "high" rock islands, and additionally in the Wallabi Group, eolianite islands. The eastern margins of the platforms have composite islands as the most abundant type. "High" rock islands typically have coastal exposures of reef and reef flat facies (bindstone with some framestone), occasionally overlain by erosional remnants, 1-2 m thick, of a basal, well bedded skeletal grainstone. The eolianite islands consist of reef facies overlain by bedded grainstone and well developed Pleistocene eolianites which, in places, are mantled by Holocene dunes. Composite islands, which overlie submerged platforms with well developed "blue-holes", consist of limited framestone, overlain by intertidal and storm ridge rudstone facies. Composite

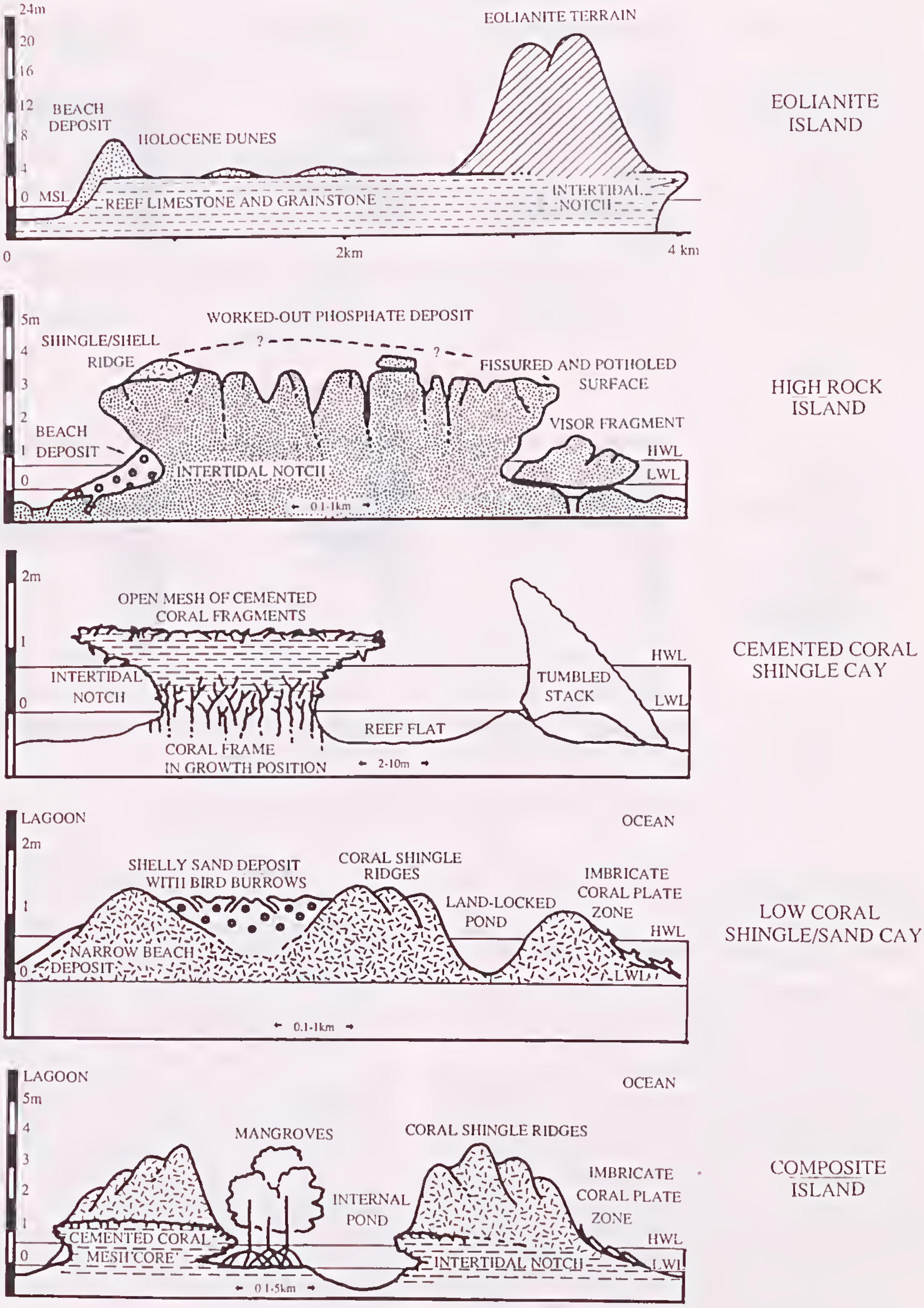

Figure 2 The morphostratigraphic characteristics of the islands in the Abrolhos platforms. Modified after France (1985).

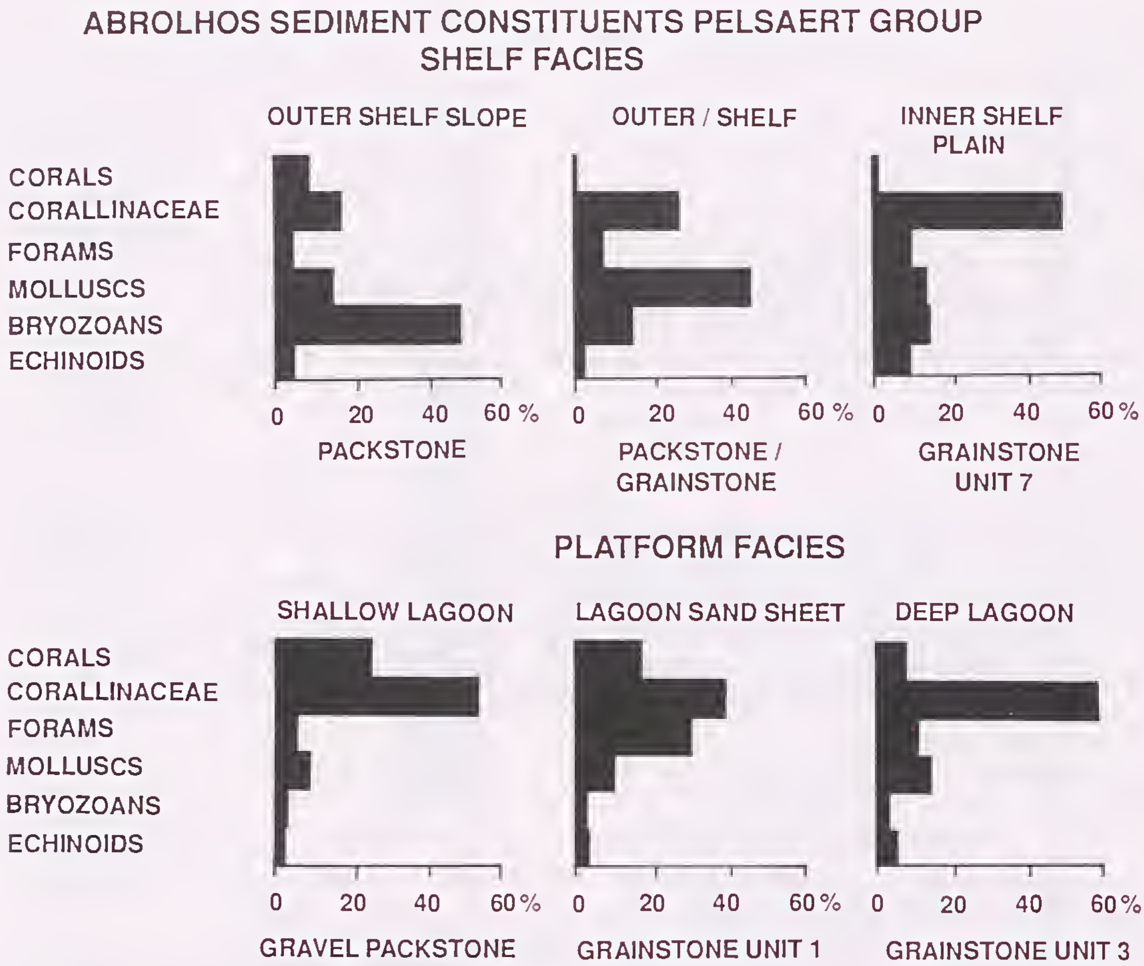

Figure 3 Holocene sediment constituents of the Abrolhos shelf and Pelsaert platform. Data modified after France (1985), and from this study.

islands are characterized by prominent surficial storm ridges composed of coral rubble.

Lagoon sand sheets and shelf sediments

Holocene skeletal sediments are present on the shelf surrounding the Abrolhos platforms, and on the platforms as shallow lagoon sand sheets and deep lagoon sand sheets. Shelf sediments thinly veneer rocky substrates. Shallow lagoon sand sheets range from a few centimetres to up to 3 m thick. The thickness of deep lagoon sand sheets is unknown but probably of similar magnitude. Sediment constituents are summarised in Fig. 3. Shelf sediments grade from inner shelf grainstones to outer shelf packstones/bindstones, and sediment composition is controlled by the resident biota, in which bryozoans and calcareous red algae are the most important elements, with minor molluscs, foraminifers and echinoids. Much of the sediment of lagoon sand sheets is generated by reef-crest communities of corals and coralline red algae (both encrusting forms and rhodolites) and is swept lagoonwards by wave- and wind-generated currents. Coralline algae and corals are volumetrically most important, with minor molluscs, foraminifers, bryozoans and echinoids.

Biotic transition

The bryozoan-coralline algal shelf sediments are distinctly temperate in character, and are regarded as foramol sediments by Lees & Buller (1972), or bryomol sediments by Nelson *et al.* (1988). Similar sediments have been described from the southern Rottnest Shelf, south of 32°S, and from the southern Australian shelf (Collins 1988). In contrast, platform sediments, composed of corals and coralline algae, have affinities with tropical/subtropical sediments (termed chlorozoan by Lees & Buller 1972) but differ in that they lack green (*Halimeda*-type) algae and non-skeletal grains such as ooids. The correlation between lithofacies, constituents and carbonate environments for a carbonate continental margin (Table 1) illustrates the transitional position of the Abrolhos platforms, which at 28°-29.5°S, form a discontinuously rimmed shelf which lies between tropical rimmed shelves to the north, and open shelves to the south. In contrast, the biotic transition between chlorozoan and foramol assemblages on the eastern Australian shelf is recorded at 24°S by Marshall & Davies (1978). There are several recorded modern examples of transition

TABLE 1

A. Correlation between lithofacies, constituents and carbonate environments (after Carannante *et al.* 1988)

Lithofacies: Lees & Buller (1972) Lees (1975)	Lithofacies: Carannante *et al.* (1988)	Key elements	Constituents	Commoner environments
Chlorozoan	Chlorozoan	Chlorophyta + Zoantharia	green algae and hermatypic corals with large benthic foraminifers, branching red algae, molluscs, etc. associated with non-skeletal grains.	tropical rimmed and open shelves
Chloralgal	Chloralgal	Chlorophyta	green algae with large benthic foraminifers, branching red algae molluscs, etc.,	
	Rhodalgal	Rhodophyta	encrusting red algae and bryozoans with molluscs, echinoids, benthic foraminifers, barnacles, serpulids, etc	transitional and/ or anomalous open shelves
Foramol	Molechfor	Molluscs + Echinoids + Foraminifers	molluscs, echinoids, benthic arenaceous foraminifers, barnacles, serpulids, etc.	cold-temperate open shelves

B. Abrolhos lithofacies, constituents and carbonate environments

Lithofacies: Lees & Buller (1972) Lees (1975)	Lithofacies: This paper	Key elements	Constituents	Commoner environments
Chlorozoan	Chlorozoan type	Zoantharia Rhodophyta	Hermatypic corals and encrusting and, branching red algae; also molluscs, foraminifers; nonskeletal grains absent	Abrolhos platforms
Foramol	Rhodalgal	Rhodophyta	Encrusting red algae and bryozoans; with molluscs, echinoids, foraminifers, etc.	Abrolhos shelf

from chlorozoan to rhodalgal lithofacies. Carannante *et al.* (1988) consider that lithofacies distribution is subject to complex environmental factors that seem related primarily to water temperature, controlled by latitude and depth.

Skeletal grain associations in warm tropical and temperate waters may be contrasted using salinity-temperature annual range diagram pairs. In Fig. 4, salinity and temperature data have been plotted for the southern Rottnest Shelf, the Abrolhos Shelf, and the

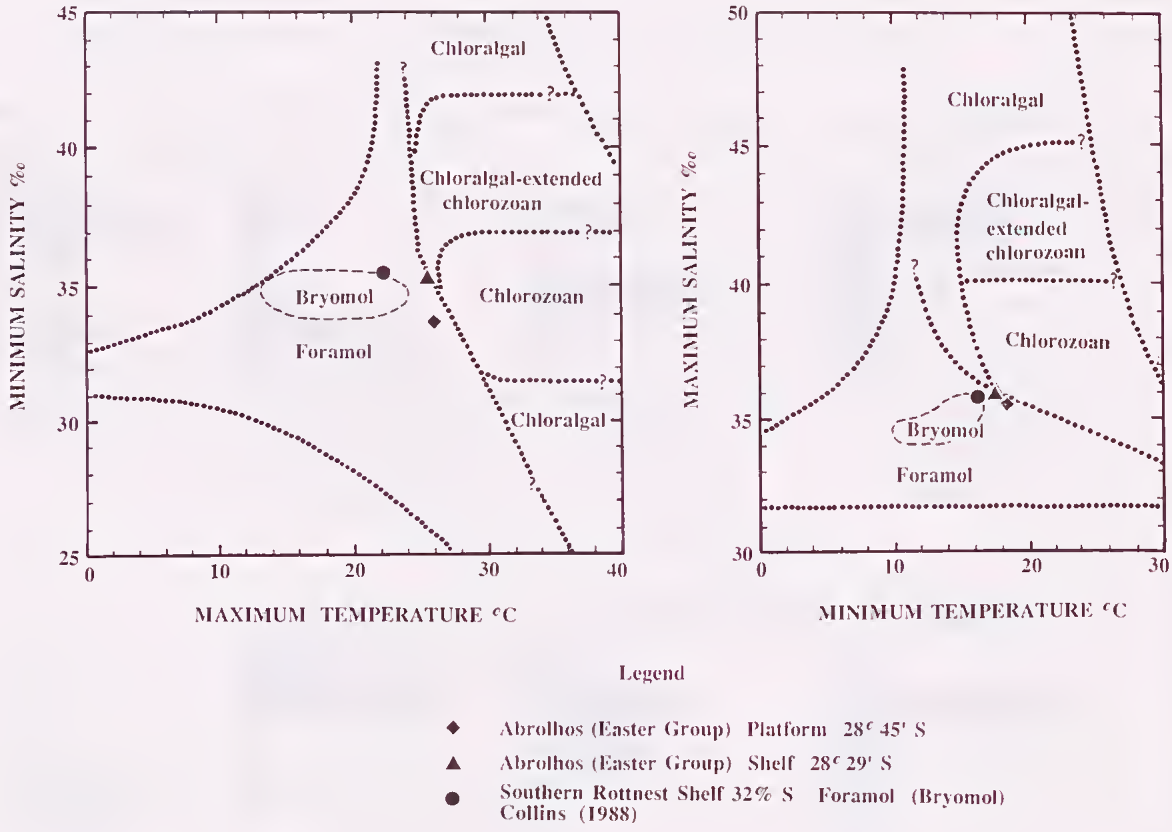

Figure 4 Salinity - temperature annual range diagram pair for southern Rottnest shelf, Abrolhos shelf and Abrolhos platform.

Abrolhos platforms (Easter Group). In contrast to the southern Rottnest Shelf, the Abrolhos data plot in a transitional position between temperate (foramol) grain assemblages and tropical/subtropical (chlorozoan) assemblages. The transitional nature of the Abrolhos platforms, as indicated by the salinity and temperature data, is supported by the data on sediment composition and biotic communities (Fig. 3, Table 1).

The Leeuwin Current clearly influences the biotic transition zone in the Abrolhos and the resultant sedimentation. Firstly, the presence of the west coast transition zone at 28 - 29.5°S, compared to the east coast transition at 24°S, is probably a direct result of the Leeuwin Current. Secondly, the presence of platform sediment with chlorozoan affinities, surrounded by shelf sediment of rhodalgal type, is a transition zone relationship for which the Leeuwin Current is probably the driving mechanism.

Initiation of reef complexes

From our present understanding of the geological history of the Abrolhos region it is clear that during the Tertiary the region saw the development of a seaward thickening carbonate wedge, dominated by bryozoan-mollusc-echinoid skeletal calcarenites and calcilutites, and lacking reef-building corals (Fig. 5). Post-Eocene carbonates were deposited as a thin sheet on a stable shelf (France 1985) and are restricted to the top 130 m of Gun Island No 1 well in the Pelsaert Group. Coral-reef-related sediments appear to be confined to the post-Eocene sequence, and the deepest coral recognised in cuttings is from - 67 m (France 1985). The shallowest of the known Tertiary sediments (Upper Eocene at 130 m) are non-reef calcarenites dominated by foraminifers, bryozoans and molluscs (Hawkins 1969).

These limited data suggest that the maximum possible thickness of the reef complex is 130 m, and that the reefs postdate open carbonate shelves of Paleocene to Upper Eocene age. There are no data to suggest that reef localisation and initiation were directly controlled by underlying geologic features. But if this is so, then it needs to be asked, why are there no prominent reef complexes between those of the Abrolhos and Ningaloo Reef to the north? The answer may after all relate to some geological substrate control, which in the case of the Abrolhos, provided a location suitable for reef development. France (1985) suggested that coralline algal biostromes similar to those of the southern Rottnest Shelf (see Collins 1988) may have provided suitable substrates for the initiation of the Abrolhos reefs. Cores up to 3 m thick have been recovered from these biostromes, which probably developed on drowned eolianite ridges (Collins 1983 Fig. 13). At the Abrolhos, there is one recorded occurrence of pre-existing eolianite topography

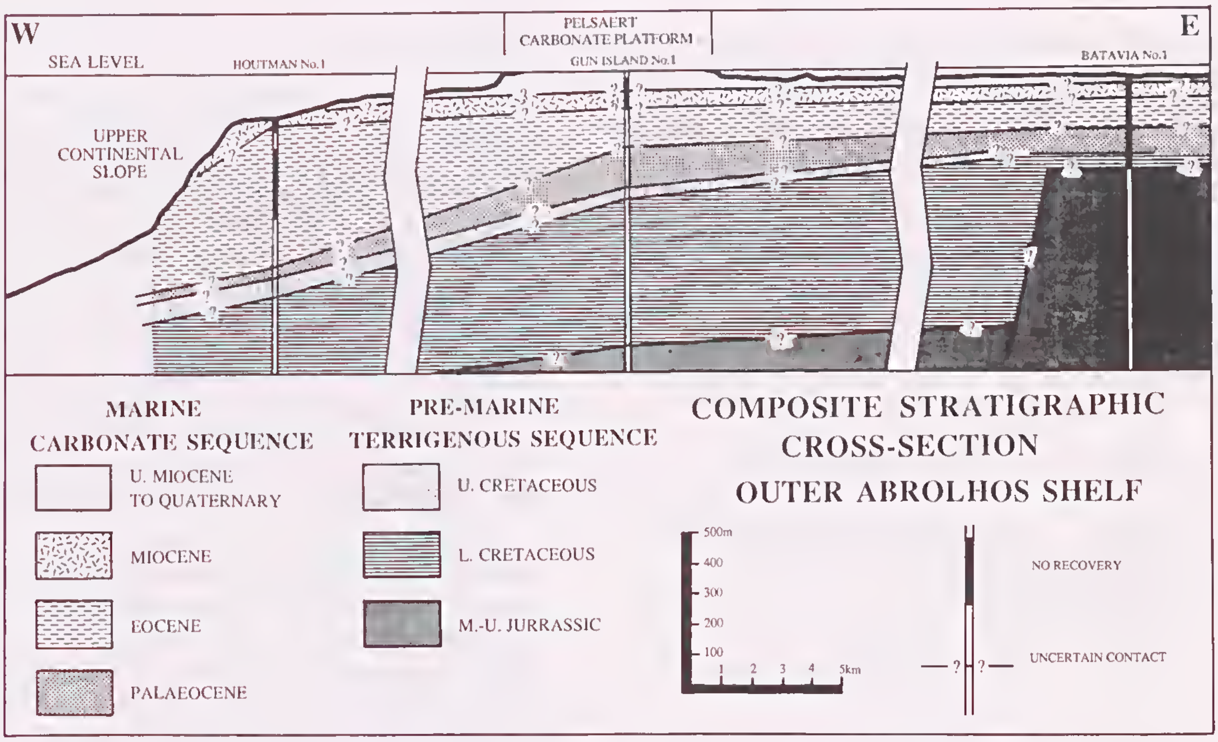

Figure 5 Diagrammatic cross-section of the Abrolhos shelf at 29.5°S. After France (1985).

underlying reef limestones of probable Last Interglacial age, at Gun Island in the Pelsaert Group.

In terms of sea surface temperature control it is not possible to ascertain whether the original development of the coral reef complex was directly due to the presence of the Leeuwin Current or whether this was linked to wider ocean-scale palaeoceanographic conditions suitable for coral reef development. However, it is clear that the persistence of the reef growth during the Quaternary must be linked to the presence of the Leeuwin Current.

There are indications in the geological record that the Leeuwin Current only came into existence during the Early to Middle Pleistocene (Kendrick *et al.* 1991). In the Perth Basin there was a conspicuous change in sedimentation from a Pliocene - Early Pleistocene, essentially siliciclastic suite of sediments, to a later Quaternary, strongly carbonate style of sedimentation.

The shift to a predominantly carbonate environment of deposition was accompanied by higher sea surface temperatures than those which prevailed during the Early Pleistocene. Evidence is found in the Middle Pleistocene mollusc fauna, which indicates greater tropical and subtropical affinities. The details of this are discussed by Kendrick *et al.* (1991). There is only a weak representation of such elements in the mollusc fauna of the older Plio-Pleistocene units, which suggests that the Leeuwin Current was then either of lesser importance than during the Middle Pleistocene, or not active.

Late Quaternary stratigraphy, reefs and geological evolution

The stratigraphy of the Abrolhos platforms is well exposed in coastal sections of the platform islands (Fig. 2) and a composite summary of the lithostratigraphy is given in Fig. 6. Four unconformity-bounded sequences have been identified, three of probable Late Pleistocene and one of Late Holocene age. At present our chronostratigraphic control on the stratigraphy is limited. A number of U-series dates are available for the lower bindstone / framestone/ rudstone unit of Fig. 6. These dates give a Last Interglacial age (*ca* 125 ka BP - Veeh & France 1988 and our preliminary dates) for this unit. This Last Interglacial unit appears to be widespread and dominates much of the geomorphology of the island groups. This conclusion was anticipated by Teichert (1967) who noted that the 100 ka BP data on the coral reef at Rottnest (subsequently revised to *ca* 125 ka BP - see below), implies that the fossil reefs of the Abrolhos will prove to be of the same order of age. However, we stress the preliminary nature of our results and would not be surprised if our stratigraphic inferences need to be revised once more numerical dates become available. The only other numerical dates that are available at present are for Holocene storm ridge units in the Pelsaert Group which show that these are Late Holocene in age. In addition, an emergent coral-frame fringe present along some islands in the Easter and Pelsaert Groups was dated at Pelsaert Island by U-series to 4.8 ka BP (Veeh & France 1988) and ^{14}C to 4.2 ka BP.

The predominance of emergent Pleistocene reefs at the Abrolhos, and thin, discontinuous veneers of Holocene reef overlying this substrate, is in marked contrast to the Great Barrier Reef. Intensive drilling investigations have shown that though Holocene reefs of the GBR are of variable thickness (4-20 m), there is usually a significant buildup of Holocene reef which overlies a buried Pleistocene substrate (Marshall & Davies 1978).

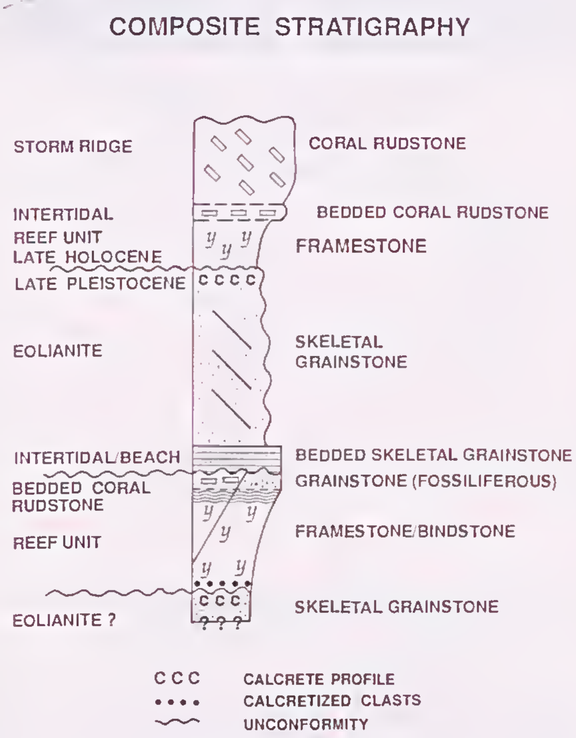

Figure 6 Late Quaternary composite stratigraphy of islands in the Abrolhos platforms.

Late Quaternary sea levels

Over the duration of the Quaternary, global sealevels have fluctuated from around their present height to more than *ca* 150 m below present sealevel (Shackleton 1987). The details of these fluctuations are complex and regionally variable. A summary of our present understanding of the Pleistocene sealevel history of the Western Australian margin is given by Kendrick *et al*. (1991), and mechanisms of Late Quaternary sealevel change are discussed by Lambeck (1987) and Lambeck & Nakada (1990). Clearly the growth history of the Abrolhos over the last few hundred thousand years is closely linked to these sealevel fluctuations.

Evidence for sealevel changes is widespread and coral reefs have proven to be especially informative, the most spectacular of these being the coral staircase of the Huon Peninsula of Papua New Guinea (Bloom *et al*. 1974, Chappell 1974). In Western Australia the reef complexes fringing the western flank of the Cape Range are also striking indicators of former sealevel events (Van de Graaf *et al*. 1976, Veeh *et al*. 1979, Kendrick *et al*. 1991).

Fig. 7 shows global sealevel for the period 135 ka BP to present; this time period represents an interglacial-glacial-interglacial cycle during which sealevels for the most part have been well below their present height. Global climates have been characterized by such glacial-interglacial fluctuations for at least 2.5 million years (Berggren *et al*. 1980). Although it is clear that the periodicity of these events will have changed in that time, it is apparent that sealevel for much of these periods will have been well below its present height. Consequently, much of the geological development of the Abrolhos reef complex was linked to sealevel stands below that of present, and there are clear indications of this in the bathymetry of the region.

From our present understanding of Pleistocene sealevel events along the Western Australian coast (Kendrick *et al*. 1991), it is clear that sealevel was close to its present height a number of times since the Early Pleistocene. And provided the tectonic controls allowed this, it is possible that elements of the emerged geomorphology of the reefs dates from these events, of which the Last Interglacial (*ca* 125 ka BP) was the most recent Pleistocene highstand. The Last Interglacial saw global sealevels probably some 5 m higher than present (*eg* Bloom *et al*. 1974, Chappell 1974, Ku *et al*. 1974, Szabo 1979). Along the coast of Western Australia the Last Interglacial dominates much of the coastal geomorphology. Consequently, it is not surprising that morphostratigraphic units of this age dominate the geomorphology of the Abrolhos reef complex.

Coral growth fluctuations

There appears to be a sharp contrast between the pattern of development of Last Interglacial and Late Holocene reefs. Coral framestone to rudstone and coralline algal bindstone facies of probable Last Interglacial age are widespread over the three platforms, as tabular developments of reef complex in excess of 10 m thick. Late Holocene coral reef development is largely restricted to leeward reef slopes, walls of "blue-holes", and leeward, more easterly surfaces of platforms, where emergent reef facies underlie prograding storm ridges, composed of coral rubble, as part of elongate, composite islands. Whilst it is tempting to suggest that the thicker and more widespread Last Interglacial reef facies indicate stronger Leeuwin Current activity and reef growth, the contrasting pattern of Last Interglacial/Late Holocene reef development may also be a function of substrate factors. The importance of antecedent topography in controlling subsequent coral reef growth is a classic theme in studies of reef geomorphology (*eg* Bloom 1974, Guilcher 1988), and in the case of the Abrolhos, the significantly higher Last Interglacial sealevels were a major determinant of Holocene reef growth patterns. However, there are also clear regional-scale data which point to stronger Leeuwin Current activity during the Last Interglacial.

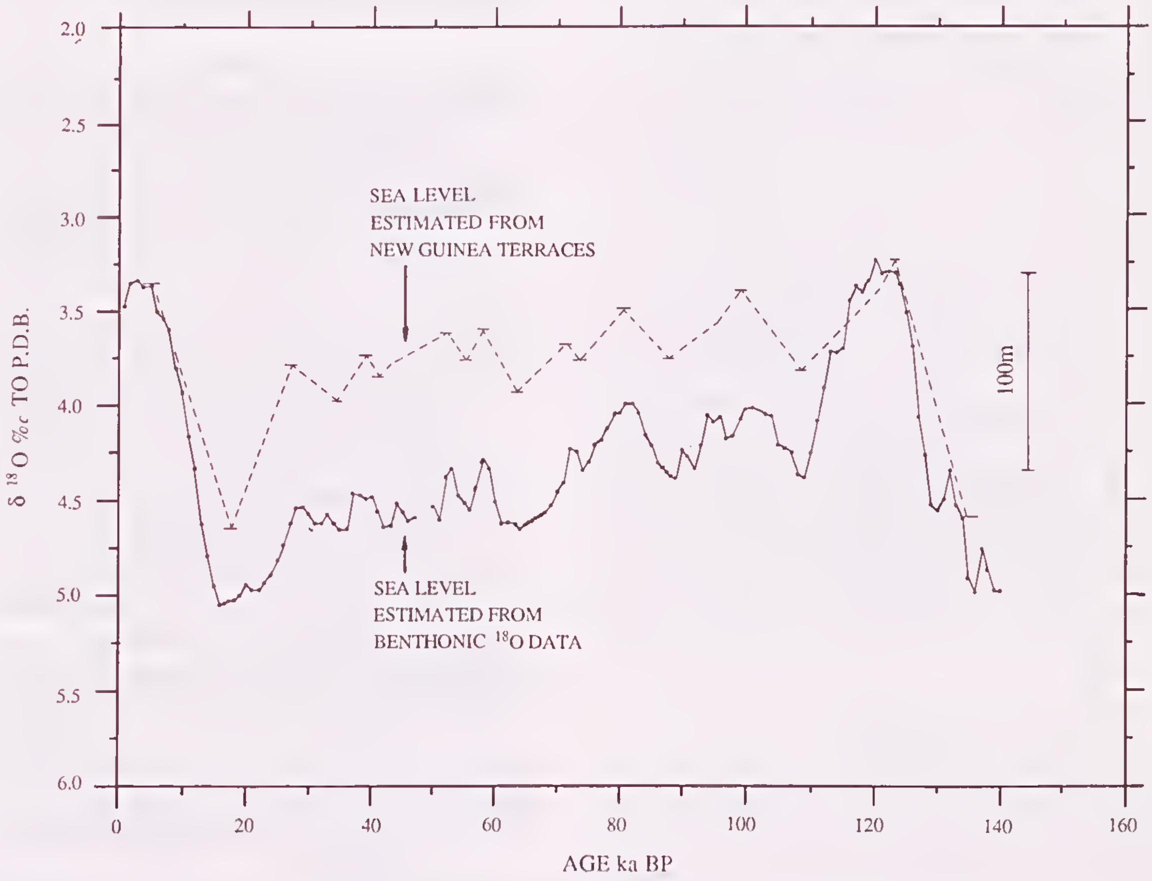

Figure 7 Benthonic oxygen isotope record of East Pacific core V19-30 for the past 140 ka and the sealevel record from the Huon Peninsular, New Guinea (after Chappell & Shackleton 1986).

The Last Interglacial was a time of widespread coral reef development along the coastal margin of much of the Perth Basin. The best known example of this is the *Acropora*-rich Rottnest Limestone (Teichert 1967, Szabo 1979, Playford 1988), 20 km offshore. This has a counterpart on the adjacent mainland in an extensive coralline - algal reef limestone with *Acropora* spp, and other warm water corals, located at the entrance to Fremantle Harbour (Skwarko 1990). These corals occur some 400 km south of their effective modern range limit at the Houtman Abrolhos. Other occurrences of *Acropora* spp. from that time extend to Augusta and eastwards to about latitude 119 °E (Kendrick *et al.* 1991). There are also clear indications in the mollusc assemblages of that time of distributional shifts, with the assemblages showing a greater tropical affinity; Kendrick *et al.* (1991) discuss this at some length.

From the southward extension of temperature-sensitive coral growth, Kendrick *et al.* (1991) argue that during the Last Interglacial sea surface temperatures along the inner shelf were higher than today, to the extent that in the Perth region inshore surface temperatures were at least 2°C higher than the 16.5°C minimum of today (Pearce *et al.* 1989).

From available evidence (discussed by Kendrick *et al.* 1991) it would seem that after the Last Interglacial highstand, sealevels along the coast of Western Australia did not again attain their present height until the Holocene. This conclusion corresponds with the generally accepted view of global sealevel in that time (Fig. 7). It is likely that the linear-ridge structures of the Abrolhos fore-reef may represent drowned reefs corresponding in age to relatively high sealevel during the last 120 ka (Fig. 7). Drowned reefs have been widely recognized in the tropical oceans (see Carter & Johnson 1986), and invariably have proven difficult to date.

The most recent work shows that at the height of the Last Glacial Maximum (*ca* 18 ka BP) global sealevel was some 130 m below present (Fairbanks 1989). Whilst the presence of linear ridge - drowned reef forms west of the Abrolhos at depths of up to 115 m (Harris 1989) implies that at the time of their formation, reef development and coral growth were still possible, the age and composition of the structures is unknown, and it is likely that sea surface temperatures were too cold for coral growth during lowstand conditions. From Indian ocean-scale paleoceanographic reconstructions (Prell *et al.* 1980) it is thought that at the Last Glacial Maximum sea surface temperatures along the coast

of Western Australia were significantly lower than present and that the cold Western Australian Boundary Current was stronger. Changes of the order of -4°C are suggested for February and August sea surface temperatures (Pearce 1991). But the cores on which these conclusions were based are few in number and were located in deep water well off the shelf. The lack of geographical resolution in this work makes it impossible to use it to establish the presence or absence of a Leeuwin Current at that time. A firm conclusion that does emerge from this work is that of a much strengthened and persistent cold boundary current off Western Australia. This makes cold water incursions on to the shelf and nearshore zone more likely. Furthermore, the dominance of cold water in the eastern Indian Ocean and a reduced flow of Western Pacific water through the Indonesian Archipelago would seem to make the functioning of the Leeuwin Current at the Last Glacial Maximum much less likely. The full implications of these changes could be firmly evaluated by the numerical models which have been used to explore the controls of Leeuwin Current formation (*eg* Batteen & Rutherford 1990, Godfrey & Weaver 1991).

Conclusions

A detailed stratigraphic and associated chronological data base is still being acquired for the Abrolhos carbonate platforms. Despite this limitation some important generalisations can be made concerning the role of the Leeuwin Current in platform and reef development, and the contrasting Late Quaternary stratigraphy of the Abrolhos reefs and eastern Australian reefs.

The widespread development of Last Interglacial coral reefs along the western continental margin to latitudes as far south as 34.5°S, and molluscan faunal data, support a period of vigorous Leeuwin Current activity. The emergent coral-algal reefs of the central and western islands of the Abrolhos have been confirmed as an important part of this system. The distribution of known Holocene reefs is, in contrast, far more limited, both in areal extent and latitudinally; the most southerly significant reefs being at the Abrolhos at latitude 28.5°S. These differences are probably largely due to fluctuations in Leeuwin Current activity. The Abrolhos reefs are characterised by widespread emergent Pleistocene substrate, consisting of Last Interglacial reef facies. Holocene corals are present as thin, discontinuous veneers over this substrate. This is in marked contrast to the Great Barrier Reef, where Holocene reefs have buried the Pleistocene substrate.

Last Interglacial reef substrates, both at the Abrolhos and elsewhere along the Western Australian coast, are frequently well above MSL and therefore could not be colonised by Holocene corals. The lack of significant thicknesses of Holocene reefs, as yet assessed only in very general ways, may also reflect slow growth rates of corals (Crossland 1981) operating at the southerly limits of their environment, under the influence of the Leeuwin Current.

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Zoogeographic provinces of the Humboldt, Benguela and Leeuwin Current systems

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Abstract

The distributional patterns of inshore marine faunas of southern South America, southern Africa and southern Western Australia are discussed. They are related to the effects of the cold northward flowing Humboldt and Benguela Currents and warm southward flowing Leeuwin Current respectively. The extent and nature of zoogeographic provinces, their faunal affinities and levels of endemicity are reviewed. In South America and southern Africa, cold temperate provinces resulting from the effects of the cold currents and associated upwellings act as barriers to dispersal of warm water faunas especially along the southwestern coasts. A corresponding cold temperate province is absent from southwestern Australia and warm water species are distributed farther south than in South America and Africa.

Introduction

Surface current patterns in the Atlantic, Pacific and Indian Oceans are characterized by major gyres that flow along the oceanic boundaries in a clockwise direction in the northern hemisphere and counter-clockwise in the southern hemisphere. The cold water, northward flowing Humboldt and Benguela Currents act with the prevailing winds to produce upwellings of nutrient-rich subsurface waters along the western coasts of southern South America and Africa. The high nutrient levels provide for increased phytoplankton production and so high production by zooplankton and secondary consumers such as anchovies (Tait 1968, Cushing & Walsh 1976).

The presence of a southward flowing current along the western coast of Australia that contacted the Houtman Abrolhos but did not reach the continental mainland was postulated by Saville-Kent (1897). Dakin (1919) compared temperatures at the Houtman Abrolhos with those at Geraldton, providing evidence of a warm offshore current. The presence of tropical species of marine invertebrates, especially molluscs, at the western end of Rottnest Island led marine biologists in the 1950's to conclude that there must be a current bringing planktonic larvae of tropical species south from areas such as the Houtman Abrolhos. It was not until 1980 that the Leeuwin Current was described (Cresswell & Golding 1980).

Current systems have major effects on the distributions of marine biota (Sverdrup *et al.* 1942, Ekman 1953, Briggs 1974, Cushing & Walsh 1976). Currents significantly influence the dispersal of organisms, especially of larval stages. Also, they determine the ambient conditions along much of the inshore environment, particularly with respect to water temperatures, salinity and nutrients. As a result, they permit survival of species in areas that would otherwise be unsuitable. Conversely, they can act as barriers to settlement by distributing organisms away from suitable habitats or by causing otherwise suitable habitats to become sub-optimal or uninhabitable.

The oceanography of the Humboldt, Benguela and Leeuwin Currents is discussed in detail by Pearce (1991) and is only briefly noted here. This paper summarises the effects of these currents on faunal distributions, and hence zoogeographic provinces, of the southern shores of South America, Africa and Australia (Fig.1). The three regions are discussed in turn and subsequently compared. The currents primarily influence southwestern coasts of the three continents but to discuss their effects relative to areas at similar latitudes with differing currents, eastern shores at the same latitudes are mentioned more briefly.

The marine biota of the southern oceans is poorly known relative to that of the northern hemisphere. Discussion of faunal distributions must therefore be circumspect. The concept of biogeographic provinces or zones remains a somewhat contentious one and indeed there is no quantitative definition of a province that has enjoyed general support. The broader principles of marine zoogeography have been discussed by many workers, foremost amongst them Ekman (1953) and Briggs (1974). In concentrating on the effects of the major currents, this paper is a simplified discussion of zoogeography in the three systems. Ambient hydrographic conditions including currents are by no means the only determinants of marine faunal occurrences. In particular, geological and long term climatological events associated with the movement of continents have had major influence upon the distributions and affinities of modern faunas. Present conditions, especially currents, act as recent

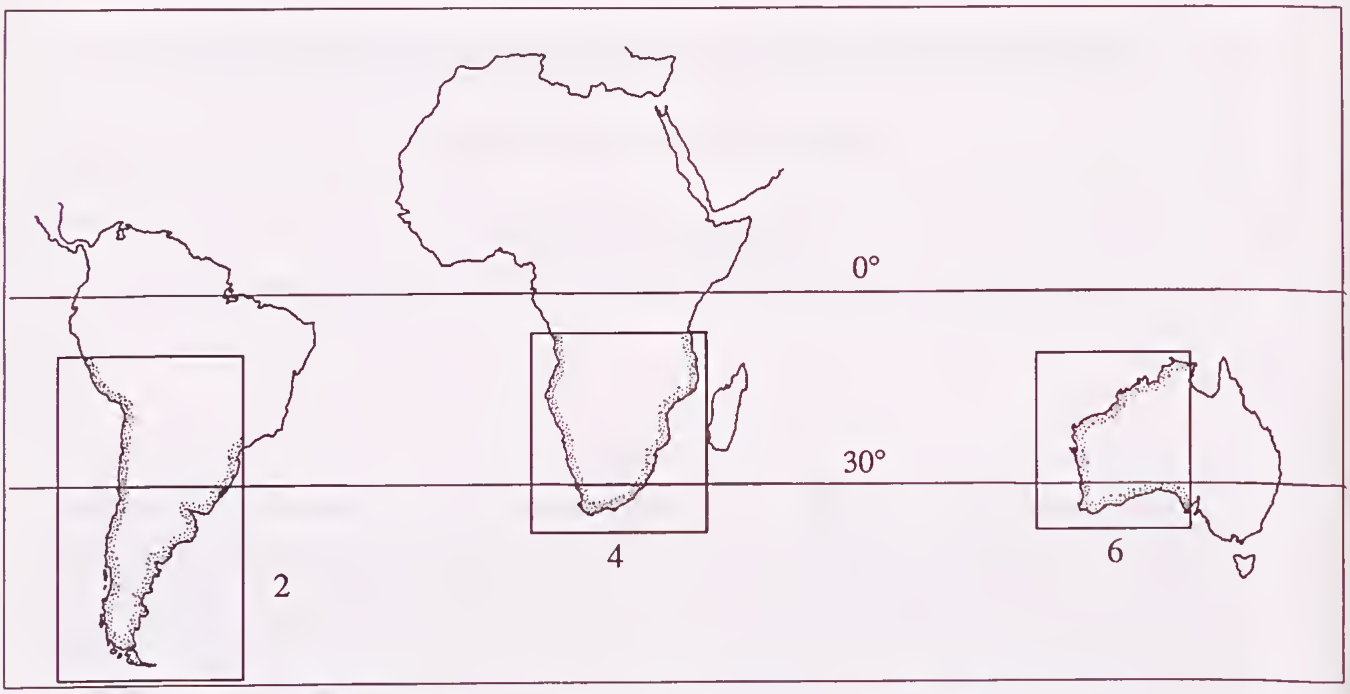

Figure 1 Regions discussed in this paper. Inserts enlarged in figures 2, 4 and 6.

modifiers of those longer term processes. The provinces here discussed are taken from the recent literature.

We have attempted to incorporate data on a wide variety of taxa but our personal interests result in a bias towards crustaceans and molluscs. The Humboldt, Benguela and Leeuwin Currents are surface currents and have limited direct influence on deeper waters. As such, this discussion is restricted to faunas of the intertidal and subtidal zones to about 200m depth.

South America

Currents: Extending south to 56°S, the western coast of Peru and Chile is contacted directly by the West Wind Drift that splits into the northward flowing Peru, or Humboldt, Coastal Current and the southward flowing Cape Horn Current that skirts the Cabo de Hornos and flows northward along the east coast as the Falkland Current (Fig.2). The Humboldt Current usually contacts the west coast at 41-46°S but in winter it may develop as far north as 32°S. The northward progression of this current and the prevailing southwesterly winds result in major upwellings of cool waters to the surface along most of the central and northern Chile coast.

In apposition to the Humboldt Current, warmer subtropical water is transferred south by the surface Chile Coastal Counter-current. The southern penetration of this current usually reaches to 37°S in summer and only 31°S in winter. At the Subtropical Convergence (23-25°S in winter, 33-34°S in summer), the Humboldt Current flows under this warmer water.

The net effect of water current movements is that there are relatively small differences in water temperatures over large distances of the Chile-Peru coastline (Brattström & Johanssen 1983).

Provinces: The relatively constant hydrographic conditions along the coast of southwestern South America (Brattström & Johanssen 1983, Brattstrøm 1990) suggest that biotic distributions should show

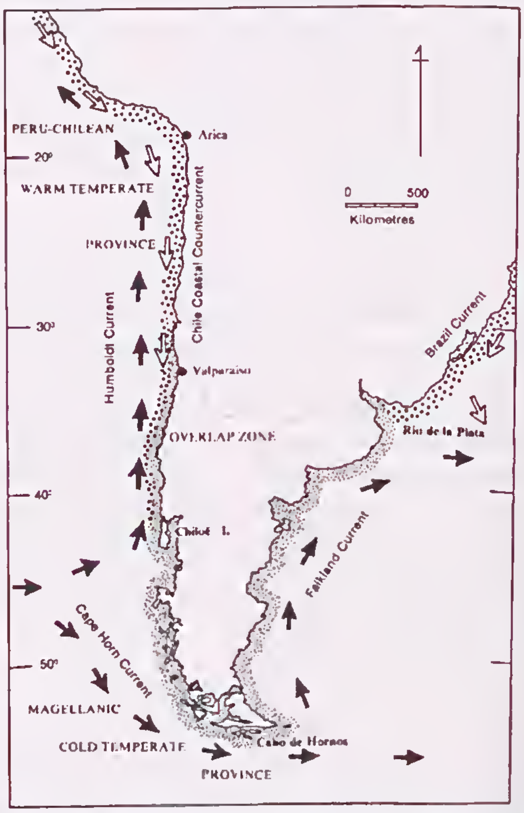

Figure 2 Zoogeographic provinces of southwestern South America. Cold currents indicated by solid arrows, warm currents by open arrows. (After various authors especially Briggs 1974, Brattström & Johanssen 1983).

clinal rather than sudden changes in composition. Indeed, most intertidal and shallow-water species have very large ranges along this coast (Brattström 1990). However, the distribution patterns for many taxa support the recognition of two zoogeographic provinces, one cold temperate (or antiboreal), the other warm temperate (Fig. 3).

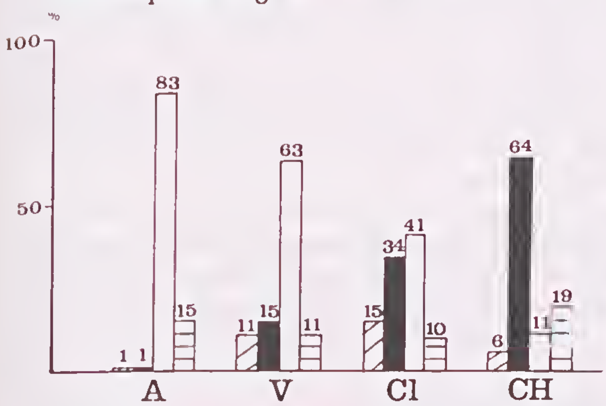

Figure 3 Composition of fauna (mixed taxa) along southwestern coast of South America.
▨: endemic species; ■ :species with southern affinities; □ :species with northern affinities; ⊟ :other. A: Arica; V: Valparaiso; Cl: Chiloé Island; CH: Cabo de Hornos. (Calculated from data of Brattström & Johanssen 1983).

South of about 42°S, the northern end of Chiloé Island, the faunal assemblages show cold temperate affinities and this province is usually known as the Patagonian or Magellanic Province. Its northern border corresponds closely with the position of impact of the Humboldt Current on the South American coast. It is recognised that the southeastern coast of South America is also cold temperate but there is some uncertainty whether or not the southeastern and southwestern coasts should be regarded as a single or as two provinces, separated at the Cabo de Hornos.

The warm temperate province, known variously as the Peruvian, Peruvian-Chilean or Peru-Chilean Province, is recognised as extending from 2-6°S south to somewhere between 30° and 42°S. The close approach of this province to the equator is a result of the upwellings and movement of cold water by the Humboldt Current.

The southern boundary of the Peru-Chilean Province is open to some interpretation. There seems little doubt that a change in faunal composition occurs at or near 42°S, evident in the distributions of decapod crustaceans (Rathbun 1910, Haig 1955, Garth 1957), echinoderms (Madsen 1956, Bernasconi 1964), polychaetes and ostracod crustaceans (Hartmann-Schröder & Hartmann 1962), molluscs (Dall 1909, Stuardo 1964, Dell 1971, Marincovich 1973), fish (Norman 1937, Mann 1954) and mixed taxa (Semenov 1977, Brattström & Johanssen 1983). From the study of Brattström & Johanssen (1983), approximately 25% of shelf benthic invertebrates have their northern or southern boundaries at or very near 42°S.

In addition to the effects of currents at this point, the topography of the coast north and south varies. North of 42°S there are no archipelagos, few islands or sheltered bays and the rocky and sandy beaches are exposed to the open ocean. South of 42°S, the coast is fringed by archipelagos of thousands of islands, is split by narrow sounds and fjords and has more sheltered beaches and mudflats.

Most workers have acknowledged a biogeographic transitional zone extending from 42°S to somewhere between 38 and 30°S (see Brattström & Johanssen 1983: fig.18). Many cold temperate species from the Magellanic Province extend into the Peru-Chilean, though few reach farther north than 30°S. This southern component is replenished by dispersals in the cold water of the northward flowing Humboldt Coastal Current. Most species in this region, however, are warm temperate. Some workers have regarded the transition zone as a separate province (*eg* Knox 1960: Central Chilean Province) but most agree with Dahl's (1960) observation that characterization of a province by a strong endemic element is lacking. Brattström & Johanssen (1983) argued that the transitional area, having a preponderance of warm temperate species, is part of the Peru-Chilean Province. It could also be suggested that it is an overlap zone of the two provinces, similar to that proposed for western Australia. Balech (1954) and Brattström & Johanssen (1983) attributed the transitional zone to variations in the relative effects of the cold Humboldt Current and warmer Chile Coastal Counter-current. There is little variation in hydrographic conditions south of 42°S.

The proportion of endemic faunas varies considerably between taxa. For the warm temperate Peru-Chilean Province, endemicity of 23-53% has been recorded for littoral molluscs (Dall 1909) and decapod crustaceans (Haig 1955, Garth 1957) and Briggs (1974) suggested that at least 50% of fish may be endemics. For the cold temperate Magellanic Province, including both southwestern and southeastern coasts, endemicity figures are generally higher with estimates of 33-61% for anomuran and isopod crustaceans, echinoderms, bivalve molluscs and fish (Ekman 1953, Haig 1955, Madsen 1956, Soot-Ryen 1959, Menzies 1962, Pawson 1969, Briggs 1974).

As was noted above, there is some uncertainty as to the southern boundary of the Magellanic Province. Stuardo (1964) suggested that Cabo de Hornos might be regarded as a boundary between two cold temperate provinces. Other authors have suggested several cold temperate provinces for South America, either with a border at Cabo de Hornos (Balech 1954) or with the southernmost landmass of the continent on both sides of the Cabo de Hornos in one province and a further cold temperate province adjoining to both the east and west (Forbes 1856, Knox 1960). Most authors have treated the southwestern and southeastern coastline as belonging within a single province (Briggs 1974) although the southeastern fauna is much less well known. The northern boundary of this province on the

east coast is generally regarded as coinciding with the Rio de la Plata at 35°S where the cold Falkland Current diverts to the east as it contacts the warm Brazil Current. An Eastern South American Warm Temperate Province is recognisable from 35°S to approximately Cabo Frio at 23°S but the composition of this fauna is very poorly known (Briggs 1974).

Summary: The major provincial boundary of cold temperate faunas of southwestern South America coincides with the normal point of impact of the Humboldt Current. This current flows north, dispersing cold water and southern species while the Cape Horn Current flows south. The point of divergence of currents acts as a fairly effective barrier to dispersal of inshore species. The contrasting effects of the Humboldt Current and Chile Coastal Counter-current result in an overlap zone between cold and warm temperate provinces between 30° and 40°S. The Humboldt Current extends the warm temperate conditions much farther north on the western coast (approximately 3°S) than the Falkland Current does in the east (about 23°S) (Fig.2). Thus tropical faunas range much farther south along the eastern coast than along the western.

Southern Africa

Currents: At about 35°S, the southern tip of Africa at Cape Agulhas is 20° farther north than Cabo de Hornos of South America. Nevertheless, it is affected by the cold water northward flowing Benguela Current (Fig.4). The Benguela Current and the prevailing southeast trade winds result in major upwellings along the southwest coast bringing cold sub-surface waters from 100-300 m to the surface. The Benguela Current flows northward into the Gulf of Guinea, where it encounters the warm Angola Current flowing southeastward, and then continues near the Equator as the now warm South

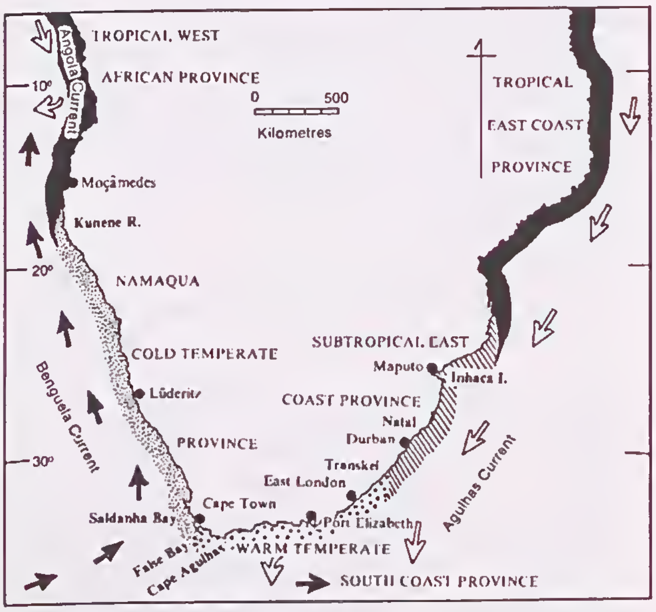

Figure 4 Zoogeographic provinces of southern Africa. Currents as per Fig. 2. (After Brown & Jarman 1978, Kensley 1981).

Equatorial Current. The combined effects of the cold northward flowing current and upwellings result in relatively little seasonal variation in sea surface temperatures along the southwestern coast of Africa.

In contrast, the eastern coast of southern Africa is dominated by southward flowing offshoots of the Indian Ocean South Equatorial Current. The warm water Agulhas Current flows southward along the southeastern coast to the vicinity of Cape Agulhas. Some warm water moves west around the Cape but most diverts to the south on contact with the Benguela Current.

Provinces: There is a substantial literature relating to the faunal provinces of southern Africa (Briggs 1974, Brown & Jarman 1978). Early workers (Forbes 1856, Woodward 1856, Ortmann 1896) suggested that a single province extends from Angola or South West Africa (Namibia) to the vicinity of Durban. Ekman (1935) regarded this province as warm temperate. Stephenson (1947), Hedgpeth (1957) and Knox (1960) divided the coast into a cold temperate province extending from the tropics of west Africa to Cape Town and a warm temperate province east of Cape Town and best developed between Cape Agulhas and Port Elizabeth. Ekman (1953) and Briggs (1974) regarded the southwestern province as a second warm temperate one; Briggs discussed the Southwestern Africa Province from Moçamedes, Angola (15°S) to Cape Peninsula (34°S) and the Agulhas Province from Cape Peninsula east to Port Elizabeth (34°S). Briggs cited the level of endemicity of the Southwestern Province to be considerably lower than that of the Agulhas Province with figures of 17% and 34% respectively (taken from Ekman (1953), based upon Stephenson's works).

More recent papers (Brown & Jarman 1978, Kensley 1981, 1983, Kilburn & Rippey 1982) supported the existence of both warm and cold temperate provinces, with a subtropical province on the east coast north of East London. The names and precise boundaries of the provinces differ between workers, the latter at least in part due to differences in distributions between taxa. For the purposes of this discussion, the provinces of Brown & Jarman (1978) and Kensley (1981, 1983) generally will be followed (Fig. 4). This pattern differs slightly from that of Kilburn & Rippey (1982) and where significant, differences are discussed.

The Tropical West African Province extends south to 20°S although Kilburn & Rippey (1982) placed its southern limit at 17°S. The fauna of Namibia is poorly known and definition of provincial borders remains speculative. The southern limit is determined by cold water effects of the Benguela Current and upwellings and typical tropical species rarely range south of this limit (Kensley 1981). Although it may be regarded as a tropical province, the influence of the Benguela Current continues a considerable distance farther north. For example, no coral reefs occur south of the equator on the west coast, the southernmost reefs being those of the Gulf of Guinea at 0-5°N. In contrast, on the

east coast coral reefs are found as far south as southern Moçambique at about 28°S.

The Cold Temperate West Coast or Namaqua Province extends from 20°S to Cape Agulhas (35°S). Kilburn & Rippey (1982) recognised an overlap zone between the Namaqua and West African Provinces, extending for 7° of latitude south of 17°S and offsetting the northern boundary of the Namaqua Province proper southwards by 4° to 24°S. The dominant influences in the province are the cold water effects of the Benguela Current and upwellings. The faunas here are more poorly known than are those to the east but are characterised by low species diversities but high populations of species present (*eg* crustaceans: Kensley 1981, 1983, molluscs: Kilburn & Rippey 1982). Productivity is high due to the nutrients brought to the surface in the upwellings. The fauna comprises few Indo-West Pacific (IWP) species and these are largely confined to the southernmost areas of the province (Kensley 1981, 1983). Atlantic-Mediterranean species proportionally dominate IWP forms amongst crustaceans and molluscs. Interestingly, the number of Atlantic crustacean species is lower in the Namaqua Province, itself situated in the South Atlantic, than in the Warm Temperate South Coast Province. The low number of Atlantic species in the Namaqua Province can be explained in terms of the water temperature regime. Water temperatures are on average warmer both north and south of the major area of upwelling at 25-30°S. The cold water of the upwellings and the northward flow of the Benguela Current act as a cold water barrier to colonisation by the more diverse tropical Atlantic faunas. Endemic species are the dominant faunal element amongst molluscs, accounting for 88% of the Namaqua species (Kilburn & Rippey 1982). Their data were pertinent only to south of the Orange River, information being too limited to speculate on endemicity farther north. The species tend not to be confined to the Namaqua Province but are endemic to southern Africa. Analysis of Kensley's (1983) data reveals that for crustaceans the endemicity is lower with 35-57% for decapods and 41-85% for peracarids, endemicity decreasing to the north. Ekman (1953) noted 17% endemicity for several taxa on the basis of Stephenson's works. Endemic fishes appear to comprise less than 20% of the fauna (Penrith 1969, Smith 1949, 1960, Briggs 1974).

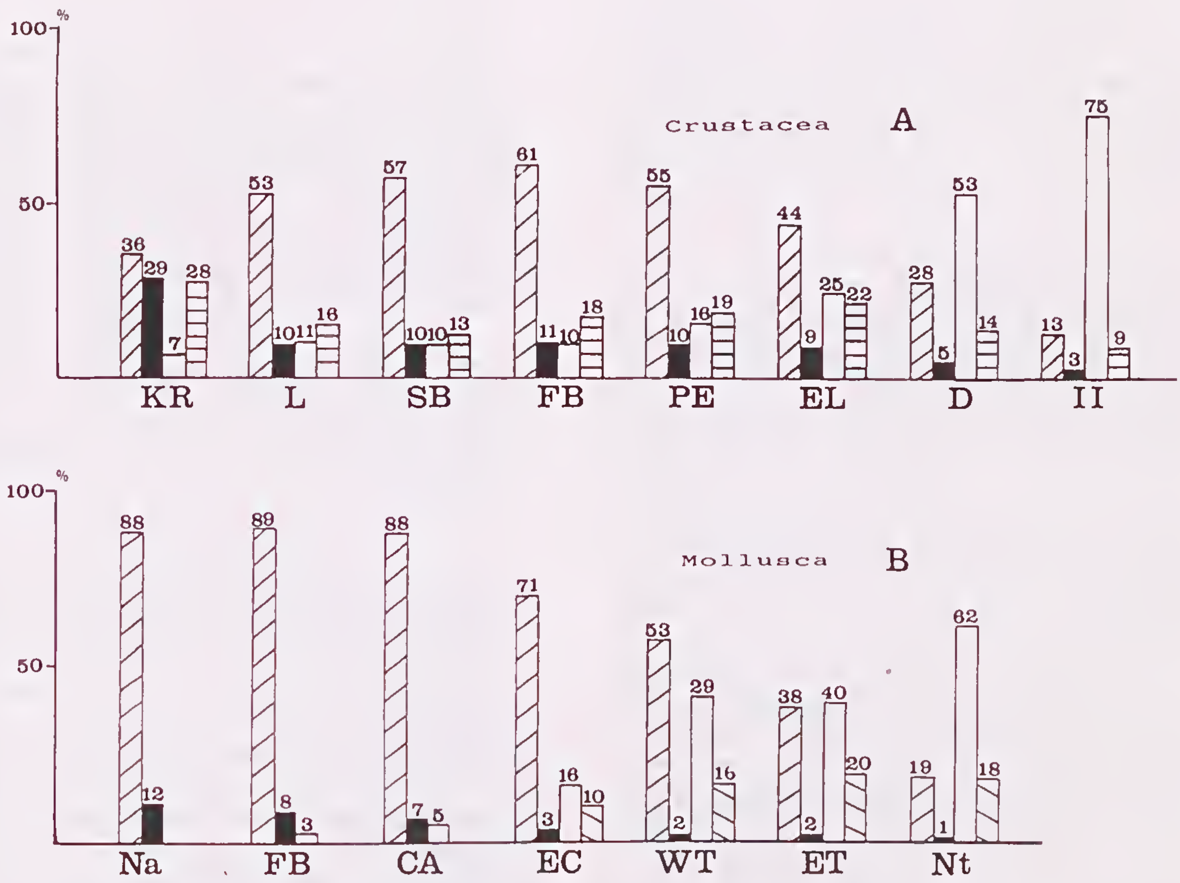

Figure 5 Composition of crustacean and molluscan taxa along southern coast of Africa.
A, Crustacea (Decapoda, Amphipoda, Isopoda combined). ▨:endemic species; ■ Atlantic-Mediterranean species; □:Indo-West Pacific species; ▤:other. KR: Kunene River; L: Lüderitz; SB: Saldanha Bay; FB: False Bay; PE: Port Elizabeth; EL: East London; D: Durban; II: Inhaca Island. (Data from Kensley 1981, 1983); B, Mollusca. As per Fig. 5A except ▨:Cape Endemics and ▧ subtropical endemics. Na: Namaqua (southern); FB: False Bay; CA: Cape Agulhas; EC: East Cape; WT: West Transkei; ET: East Transkei; Nt: Natal. (Data from Kilburn & Rippey 1983).

A south coast warm temperate province has been recognised by most workers (Briggs 1974). The Warm Temperate South Coast Province of Brown & Jarman (1978), or Algoa Province of Kilburn & Rippey (1982), extends in an east-north-east direction from an overlap zone between Cape Town to Cape Agulhas to just north of East London. Species diversity and, not surprisingly, the number of IWP species is higher than in the Namaqua Province. For peracarid crustaceans, this province is the most diverse in southern Africa. The proportion of IWP molluscs decreases progressively from east to west, reaching their western limits at False Bay/Cape of Good Hope (Kilburn & Rippey 1982) (Fig.5).

The numbers of Atlantic species are as high as or higher than in the Namaqua and as proportions of the total number of species, Atlantic representation can be as high or only slightly lower. The increase in Atlantic species to the east of Cape Agulhas, at least in the Crustacea, may be explained by at least two processes. Some species may represent relict populations of more diverse faunas present in the warmer Pleistocene Period. Others are likely to be more recent migrants, distributed by some movement of South Atlantic waters around Cape Agulhas (Shannon 1966) or by the large gyre circulation of Atlantic water into the South Equatorial Current of the Indian Ocean and thence southwest into the Agulhas Current. The warmer conditions of the Warm Temperate South Coast Province are more suitable for recruitment of many Atlantic species. The number of species endemic to southern Africa is very high. Endemics account for 33-54% of decapod and amphipod crustaceans, 88-92% of isopod crustaceans and 38-70% of molluscs (Kensley 1981, 1983, Kilburn & Rippey 1982, Gosliner 1987), with the proportion of endemics generally decreasing to the east. High endemicity has also been recorded in this province for hydroids (Millard 1978), soft corals (Williams 1990), ascidians (Millar 1962), fishes (Smith 1949, 1960, Penrith 1969) and mixed taxa (Ekman 1953, Day *et al.* 1970). Day (1978) and Kensley (1983) suggested that the province has been a centre of evolutionary radiation for crustacean groups with ancestral stock from both Atlantic and IWP origins; Millard (1978) proposed a similar evolutionary centre for hydroids.

The Subtropical East Coast Province extends from an area of overlap with the Warm Temperate South Coast Province to Inhambane, Moçambique, close to the Tropic of Capricorn. Kilburn & Rippey's (1982) equivalent Natal Province has its northern boundary 6° farther south, their interpretation being that mollusc faunas north of 29°S are essentially tropical. Coral reefs appear about midway along the north-south extent of this province indicating the warm water effects of the Agulhas Current. The diversity of decapod crustaceans increases markedly but that of peracarid groups declines (Kensley 1983). The IWP and Atlantic faunal elements continue to increase and decrease respectively in both numbers of species and proportion of total species. Endemicity declines towards the north in numbers of species and proportionally for crustaceans (Kensley 1981, 1983) and molluscs (Kilburn & Rippey 1982, Gosliner 1987) (Fig. 5). In molluscs, the endemics show a shift towards tropical rather than temperate affinities. This province may also be regarded as an overlap or transition zone between tropical and warm temperate provinces (see concluding comparison of systems).

The Tropical East Coast Province ranges from the Tropic to north of the equator; Kilburn & Rippey's (1982) Indo-Pacific Province begins 6° farther south. The province is heavily dominated by IWP forms. There are very few Atlantic and few endemic species.

Overall affinities of the fauna for the African coastline south of 15°S vary somewhat between taxa. The IWP faunal element is dominant in species diversity for decapod crustaceans (61-66% of species) (Kensley 1981, 1983) while the Cape endemic component is dominant for peracarid crustaceans (46% of amphipod species, 65% of isopod species) and molluscs (19-89%, depending on locality, Kilburn & Rippey 1982) (Fig.5). The Atlantic-Mediterranean element accounts for only 5-15% of crustacean and 1-12% of molluscan species.

Summary: The Benguela Current affects the distribution of inshore faunas in several ways. It circulates cold water northwards and encourages the upwellings of sub-surface water along the southwestern coast. The current and upwellings combine to extend a cold temperate province to within 20° of the equator and form an effective cold water barrier to movement of warm water Atlantic species southwards and to warm water IWP species westwards. There is a distinct containment of tropical faunas to the north of the cold water province. The western coast tropical province has its southern boundary at least 5° farther north than its equivalent province on the eastern coast. Areas on the eastern coast at similar latitudes to that of the cold temperate Namaqua Province are subtropical or warm temperate.

Southwestern Australia

Currents: The southwestern coast of Australia extends just south of 35°S near Albany, similar in latitude to the southern tip of Africa and is therefore north of the main flow of the West Wind Drift. The southward flowing Leeuwin Current, originating to the north of North West Cape (21° 47'S), brings warm, low salinity water south around Cape Leeuwin and east into the Great Australian Bight (Cresswell & Golding 1980, Godfrey & Ridgeway 1984, Pearce & Cresswell 1985, Pearce 1991) (Fig.6). The Leeuwin Current usually peaks in the winter, becoming weak in summer. It flows along the outer continental margin off the coast, intercepting offshore islands but not the inshore continental coastline until the Cape Naturaliste-Cape Leeuwin area. Because of the Leeuwin Current there is no substantial upwelling along the southwestern coast of

Figure 6 Zoogeographic provinces of Western Australia. Currents as per Fig. 2. (After Wilson & Allen 1987).

Australia. Surface waters are nutrient poor and primary productivity is low.

The Leeuwin Current roughly parallels the East Australian Current that brings warm waters southward to about 33°S before diverting as eddies into the Tasman Sea. Thus, unlike South America and Africa, Australia has southward flowing warm currents on both western and eastern coasts.

Provinces: Biogeographic reviews of Australian marine inshore fauna, especially intertidal species, from the 1930's into the 1970's recognised five to six provinces, of which two occurred along the western coast (Whitley 1932, Bennett & Pope 1953, Knox 1963, Briggs 1974). A tropical province, the Dampieran, extended from about Shark Bay or Geraldton north and east to Cape York and a warm temperate province, the Flindersian, extended from the Dampieran south and east to western Victoria.

More recently, the marine biogeographic zonation of Australia has been simplified into a recognition of a Northern Australian Tropical and a Southern Australian Warm Temperate Province with broad zones of overlap on both western and eastern coasts that for this discussion will be regarded as the Western Coast and Eastern Coast Overlap Zones (Fig.6) (Wilson & Gillett 1971, Marsh 1976, Wilson & Stevenson 1977, Wells 1980, 1986, 1990, Wilson & Allen 1987).

The northern coast of Western Australia, northeast from North West Cape, has a tropical biota that is continuous with other parts of the Indo-West Pacific. In general, species diversity decreases with increasing latitude but there are no major distributional boundaries, most species reaching as far south as North West Cape. Endemicity is low in the Northern Australian Tropical Province with about 10% of mollusc species (Wilson & Allen 1987), 13% of fishes (Wilson & Allen 1987), 17-22% of brachyuran and anomuran decapod species (Griffin & Yaldwyn 1967, Morgan 1990), essentially no corals (Potts 1985, Veron 1985, Wilson & Allen 1987) and, for the northwestern coast, about 13% of echinoderms (Marsh 1976, Marsh & Marshall 1983) being endemic to Australia (Fig.7). The relationship of the tropical northern coast with other parts of the Indo-West Pacific has been most recently discussed by Wells (1986, 1990) and Wilson & Allen (1987).

The southern coast of Western Australia east of Cape Leeuwin (34°22'S) is part of the Southern Australian Warm Temperate Province. In addition to the effects of the weakening Leeuwin Current, the warm temperate province is influenced by the cold West Wind Drift, which has been responsible for the distribution of some widespread or circumpolar elements into the southern Australian fauna (Fell 1962, Knox 1979, Edgar 1986). IWP species representation is low and decreases from west to east. Most of the temperate species that occur along the south coast of Western Australia reach as far west as Cape Leeuwin without major biogeographic discontinuities. Rates of species endemicity are much higher in this province than in northern waters: approximately 85% for fishes (Wilson & Allen 1987), possibly 95% for molluscs (Wells 1980, Wilson & Allen 1987), 90% for echinoderms (Clark 1946, Rowe & Vail 1982) and 63% for decapod crustaceans (77% endemic to Australia) (Morgan & Jones 1991).

Fig. 7 shows the affinities of crustaceans and molluscs of western Australia. Note that for crustaceans, species endemic to Australia are plotted, accounting for a high proportion of the south coast fauna. For molluscs, south coast endemics are incorporated in the category of species with southern affinities and endemics are those confined to the four regions.

In many respects, the Western Coast Overlap Zone is a region of transition with gradual replacement of a tropical fauna in the north by a predominantly temperate fauna in the south (Wilson & Allen 1987). There is a small proportion of species endemic to Western Australia and most of these have at least part of their range in the Western Coast Zone and often achieve their greatest numbers there (Wells 1980, Wilson & Allen 1987). The proportion of endemics varies between taxa: 20% for shallow water asteroids (Marsh 1976) and less than 10% for prosobranch molluscs (Wells 1980).

Two offshore regions clearly illustrate the effects of the Leeuwin Current on faunal composition: the Houtman Abrolhos (28-29°S) and Rottnest Island (32°S).

Although it has substantial numbers of temperate species and Western Australian endemics, the fauna of

the Houtman Abrolhos is essentially tropical (Montgomery 1931, Wilson & Marsh 1979, Wells 1980, Veron 1985) and the Abrolhos is generally considered to be the southern limit in Western Australia of the tropical marine biota (Wells 1980, Wilson & Allen 1987). The southern limit of the tropical fauna in eastern Australia is usually regarded as being slightly farther north, somewhere between 26° and 27°S (Endean 1957, Wilson & Gillett 1971).

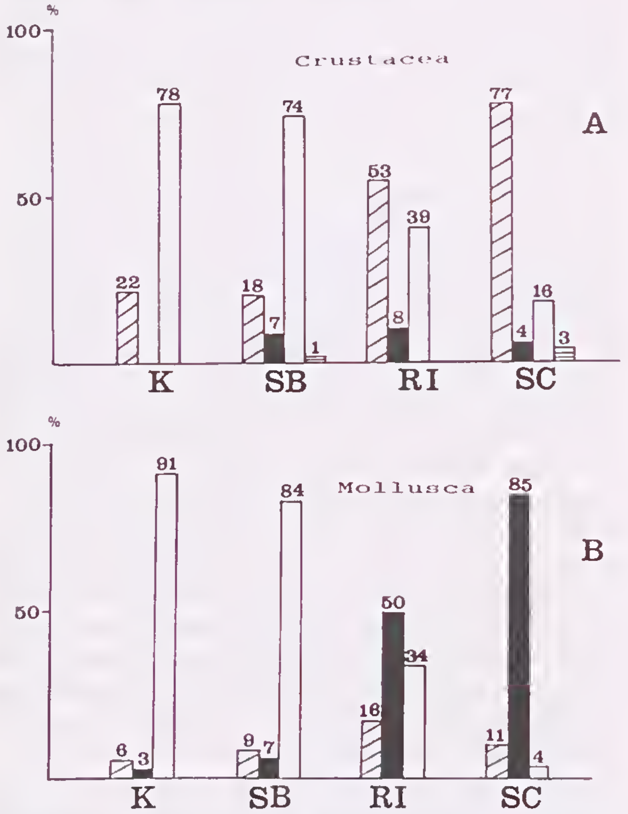

Figure 7 Composition of crustacean and molluscan taxa along western coast of Australia.
A, Crustacea (decapods only except Rottnest Island). ▨:Australian endemic species; ■:species with southern affinities (excluding south coast endemics); □:Indo-West Pacific species; ▤:other. K: Kimberleys; SB: Shark Bay; RI: Rottnest Island; SC: South Coast. (Data from Jones 1990; Morgan 1990, Morgan & Jones 1991.)
B, Mollusca. :▨ species endemic to the region, ■:species with southern affinities (including Australian south coast endemics); □:IWP species. (Data in part from Wells 1980)

Hodgkin *et al.* (1959) recorded 18 tropical invertebrate species at Rottnest Island. Hutchins (1979) found that about 26% of the 350 fish species recorded from Rottnest Island were of tropical origin and almost 40% of marine crustaceans known from the island are tropical IWP species (Jones & Morgan unpublished data) (Fig.7). The coral *Pocillopora damicornis* forms a small reef near Parker Point, the southernmost reef development in the state and one of the most southerly in the world. The fauna associated with the coral is similar to that of many tropical localities elsewhere in the world (Black & Prince 1983). The tropical *Echinometra mathaei*, the dominant echinoid at the western end of Rottnest Island, shows a continuous reproductive season typical of tropical species (Pearse & Phillips 1968). Black & Johnson (1983) reported that many of the fauna at Rottnest Island are of tropical origin.

Tropical marine invertebrates extend farther to the south, well into the Southern Australian Temperate Province. Maxwell & Cresswell (1981) have shown that larvae of tropical species can be distributed into the Great Australian Bight by the Leeuwin Current. Wells (1980) showed that 9 of 308 tropical prosobranch gastropod species examined reached Cape Leeuwin and 5 extended onto the south coast. Veron & Marsh (1988) found that 25 of 318 species of hermatypic corals reached as far south as Rottnest Island and 9 species occurred on the south coast.

Differences in composition of the fauna between inshore and offshore areas have long been known (Saville-Kent 1897, Dakin 1919). Wells (1985) found that proportions of tropical, temperate and endemic molluscs were almost identical at the eastern end of Rottnest and inshore. The proportion of endemic species at the western end of Rottnest was similar (13-16%) but the proportion of tropical species was nearly double and temperate species declined from 67% inshore and at the eastern end of Rottnest to 52% at the western end. Similarly, molluscan biomass and densities were dominated by temperate species at inshore sites while tropical species accounted for over half the biomass and density at some western end sites.

Summary: The warm southward flowing Leeuwin Current disperses tropical representatives of many taxa to the southwestern and southern coasts of Australia. No cold temperate province exists and tropical and warm temperate provinces grade into each other in a broad overlap zone. The offshore nature of the current results in higher proportions of tropical marine faunas at offshore localities than along the mainland. Due largely to the effects of the Leeuwin and East Australian Currents, the pattern of provinces is similar along the western and eastern coasts of Australia.

Comparison of Humboldt, Benguela and Leeuwin Systems

There are substantial differences between the hydrography and marine faunas of the southwestern coasts of South America, Africa and Australia. Although South America reaches fully 20° of latitude farther south than Africa and southwestern Australia, there are greater similarities in inshore water circulation between South America and southern Africa. Both show a general pattern of northward moving cool waters along their western coasts that is reinforced by a series of major upwellings. In contrast, the southwestern coast of Australia lacks both a northward flowing cold current and significant upwellings. The dominant inshore current is southward flowing and warm water. Australia is unique amongst

the mid-latitude southern continents in having a similar pattern of major currents on western and eastern coasts.

The Humboldt and Benguela Currents serve to extend temperate waters and their associated faunas much farther north than along the Western Australian coast. In South America, a warm temperate province extends north to about 3°S and in southern Africa, a cold temperate province to within 20°S. The cold waters and northward flow serve as effective barriers to southward movement of tropical west coast faunas that are restricted to only limited penetration south of the equator. The cold water conditions also restrict invasion by eastern coast tropical and warm water species, distributed much farther southward than on the respective western coasts. The Humboldt and Benguela Currents therefore act as barriers to warm water species through distributional and environmental effects.

The Leeuwin Current extends warm waters much farther south along the southwestern Australian coast. A tropical north coast province extends to about 22°S inshore and to 29°S at the Houtman Abrolhos, approximately 19° (26°) and 2° (9°) farther south than in western South America and southern Africa respectively. Many tropical species with IWP affinities are distributed southward with a significant tropical inshore faunal element evident as far south as Rottnest Island at 32°S. A number of tropical species range farther south into the Great Australian Bight. There is no distinct barrier to warm water species, tropical faunas instead gradually diminishing with increasing latitude. Coral reefs are richly developed at the Houtman Abrolhos and occur at Rottnest Island but are found no farther south than 1°28'S and 0-5°N off southwestern South America and Africa respectively (Kensley 1981, Wells 1988).

A comparison of the marine zoogeographic provinces of the three continents reveals some close similarities between the western coast of Australia and the eastern coast of southern Africa. The Northern Australian Tropical Province and the Tropical East Coast Province of Africa share high species diversity, a high incidence of tropical IWP species and low species endemicity. The Western Coast Overlap Zone of Australia and the Subtropical East Coast Province of Africa have relatively high but decreasing diversity, many IWP species and a recognisable endemic component. The Southern Australian Warm Temperate Province and the Warm Temperate South Coast Province of Africa show decreased diversity, fewer tropical species that diminish with increasing latitude and relatively high numbers of endemics. For many taxa, these provinces appear to have the highest rate of endemicity in western Australia and southern Africa and in the latter region has the highest diversity for some groups (*eg* peracarid crustaceans).

It is more difficult to make valid comparisons between western Australian and eastern South American provinces. The marine fauna of the latter region remains very inadequately described. The Brazilian Province shows high species diversity and low endemicity, broadly similar to the Australian Tropical Province. There is no recognised overlap zone between tropical and temperate provinces of eastern South America but this may reflect more the paucity of faunal distributional data rather than a real disjunction between provinces.

There is no southwestern Australian counterpart to the cold temperate Magellanic and Namaqua Provinces of southern South America and southwestern Africa. Consequently there is no corresponding drop in diversity, rise in productivity and retreat of tropical faunal elements associated with a cold water mass and upwellings. There is no distinct cold water barrier to dispersal and recruitment of tropical species.

Largely as a result of inshore circulation effects, the marine biogeographic provinces of the western and eastern coasts of South America and Africa are asymmetrical. This is particularly true for southern Africa where the cold temperate province is offset to the southwest. In Australia, the pattern of provinces is essentially symmetrical along the western and eastern coasts with relatively minor differences in the extent of provinces due to variable effects of the Leeuwin and East Australian Currents.

It is wise to conclude this review with the note of caution sounded in the Introduction. Prevailing hydrographic conditions are modifiers of faunal distributions established by long term geological and climatological processes. This can be illustrated briefly for Australia. Throughout the mid- to late Tertiary, the southwestern coast supported a high proportion of faunas originating in the late Mesozoic tropical ocean Tethys and derived IWP species. This is in contrast to southeastern Australia which then had many temperate palaeoaustral forms (Knox 1980, Darragh 1985, Wilson & Allen 1987). Most invasions of tropical species along the southern Australian coast have been from the west. The present hydrographic conditions have maintained rather than caused the relatively high tropical influence in southwestern Australia.

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The effect of sea temperature on seagrasses and algae on the Western Australian coastline

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Abstract

Macroalgae and seagrasses are the important primary producers on the West Australian coastline. As benthic organisms, they are effective integrators of the environment, but their presence at a particular location is the result of two different processes - 1) Dispersal and settlement and 2) Growth. The Leeuwin Current may affect both these processes, through its transport of reproductive material (both vegetative and sexual) and its effect on water temperatures.

Direct effects of the Leeuwin Current on the marine flora of south west Western Australia are less detectable than its effects on marine animals. Marine macroalgae show only sporadic tropical influence, with the flora being dominated by southern temperate species. The Leeuwin Current does affect tropical seagrass species in WA by extending their southern latitudinal distribution limits.

The west coast of Western Australia is very different to the east coast of Australia and to the west coasts of South Africa and South America. Macroalgae are particularly influenced by the prevailing currents and upwellings, and the Western Australian coast does not have the large, cool temperate kelps present on the other two continental west coasts. The absence of seagrasses from both these west coasts would seem to be a consequence of lack of habitat availability for seagrasses.

Introduction

Macroalgae and seagrasses are important benthic primary producers on the Western Australian coastline. They represent very different types of organisms - algae belong to the Kingdom Protista, and there are *ca* 8500 marine species world-wide, whereas seagrasses are a very specialised group of about 50 species of angiosperms that have reinvaded the marine environment. However, requiring light for photosynthesis, they are both found in relatively shallow water, and play similar roles in their coastal habitats. As benthic organisms, they are effective integrators of the environment, but their presence at a particular location is the result of two different processes:

1. Dispersal and settlement
2. Growth

The Leeuwin Current, which brings warm tropical water down the west coast of Australia in winter (Pearce 1991) may affect both these processes, through its transport of reproductive material (both vegetative and sexual) and its effect on water temperatures.

Macroalgae occur on rocky substrata, with a variety of water movement conditions. Their depth range is from the intertidal to about 50 m, although this may be greater in clear offshore areas, and less in more turbid inshore waters. Some 360 species have been recorded from Rottnest Island (Huisman & Walker 1990), but the total for the Western Australian coast is probably about 700.

The main habitats for seagrasses are very extensive shallow sedimentary environments that are sheltered from oceanic swell, such as embayments (*eg* Shark Bay, Cockburn Sound), protected bays (*eg* Geographe Bay, Frenchman's Bay) and lagoons enclosed by fringing reefs (*eg* Bunbury to Kalbarri). Seagrasses occupy approximately 20 000 km^2 on the Western Australian coast (Kirkman & Walker 1989), ranging in depth from the intertidal to 45 m (Cambridge 1980), making up a major component of nearshore ecosystems. The diversity of seagrass genera (10) and species (25) along this coastline (Table 1) is unequalled elsewhere in the world (Walker & Prince 1987).

Temperature and Biogeography: Macroalgae

In general, the rocky sub-tidal environment of south-west Western Australia has extensive populations of the kelp *Ecklonia radiata* and *Sargassum* spp. Mixed macroalgal assemblages of foliose red, green and brown algae also occur, particularly on convoluted limestone reef substrata. As the substratum changes from limestone to granite at Cape Naturaliste, cold temperate brown algae become much more

conspicuous. However, the Western Australian coast does not possess large kelps such as *Macrocystis*. To the north, the kelp disappears and more tropical genera and species become dominant eg *Dictyopteris*. The Rhodophyta become more abundant, particularly those that calcify.

Table 1

Seagrass species found in Western Australia

Amphibolis antarctica (Labill.) Sonder et Aschers. ex Aschers.
Amphibolis griffithii (J.Black) den Hartog
Cymodocea angustata Ostenfeld
Cymodocea serrulata (R.Br.) Aschers. and Magnus
Enhalus acoroides (L.f.Royle)
Halodule pinifolia (Miki) den Hartog
Halodule uninervis (Forsk.) Aschers.
Halophila decipiens Ostenfeld
Halophila ovalis (R.Br.) Hook.f.
Halophila ovata Gaud.
Halophila spinulosa (R.Br.) Aschers.
Heterozostera tasmanica (Aschers.) Dandy
Posidonia angustifolia Cambridge & Kuo
Posidonia australis Hook.f.
Posidonia coriacea Cambridge & Kuo
Posidonia denhartogii. Kuo & Cambridge
Posidonia kirkmani Kuo & Cambridge
Posidonia ostenfeldii Ostenfeld
Posidonia robertsoniae Kuo & Cambridge
Posidonia sinuosa Cambridge & Kuo
Syringodium isoetifolium (Aschers.) Dandy
Thalassia hemprichii (Ehrenb.) Aschers
Thalassodendron ciliatum (Forssk.) den Hartog
Thalassodendron pachyrhizum den Hartog
Zostera mucronata den Hartog

The southern Australian flora is well documented (Womersley 1984, 1987) and has one of the richest algal floras in the world (400 genera and 1100 species, Womersley 1984). However, the western coast has a reduced diversity in comparison to the south coast, despite the transition from the cold temperate flora to the subtropical and typically Indo-Pacific tropical flora of the northern waters. The relative absence of intensive collections and taxonomic studies of algae in the north of Western Australia does make biogeographical analyses of algal distributions difficult, but recent works by Kendrick *et al*. (1988, 1990) for Shark Bay, and Borowitzka & Huisman (ms) for the Dampier Archipelago have increased the information available for comparison. Huisman's collections from the Abrolhos Islands have also improved distribution records.

The most recent synthesis of south-western Australian algal distributions has been carried out by Huisman & Walker (1990) for Rottnest Island. They described Rottnest Island as possessing limestone reef habitats typical of the mainland coast, from Cape Naturaliste to Kalbarri, and regarded the marine flora as representative of the mainland coastline. They carried out a biogeographic analysis of the macroalgal species present (Table 2) that showed the dominance of southern Australian species, with a relatively low representation of the tropical element. This is also true for the mainland coast.

Table 2

Biogeographic affinities of algal species recorded from Rottnest Island

Distribution	Number of species			
	Rhodophyta	Phaeophyta	Chlorophyta	Total
Cosmopolitan	8	5	3	16
Indo-West Pacific	7	4	1	12
Tropical-Warm Temperate	18	10	12	40
Temperate	9	10	3	22
Southern Temperate	18	5	5	28
Southern Australian	114	31	25	170
West Australian endemic	40	5	3	48
Rottnest Island endemic	8	1	2	11
Total	222	71	54	347

While the Leeuwin Current may introduce the occasional tropical taxon to the flora, the floristic affinities of Rottnest Island lie clearly with the temperate southern coastline. Most "tropical" macroalgal species reported from Rottnest Island are of sporadic occurrence, suggesting that their appearance in the marine flora may be related to the variable strength of the Leeuwin Current. An interesting example is provided by Harvey (1855, p. 564), who recorded *Penicillus nodulosus* (as *P. arbuscula*) as "abundant, on shallow, sand-covered reefs at Rottnest". Presently, this species is found abundantly only much further north *eg* at the Abrolhos (B. Hatcher, pers. comm. 1989) or Cliff Head (Edgar, pers. comm. 1991), and has not been observed at all on Rottnest recently. Harvey's observation was made during the austral winter, when the Leeuwin Current flows most strongly, but *Penicillus* is no longer a

constituent of the marine flora of Rottnest Island at any time of year.

Temperature and Biogeography: Seagrasses

Seagrass distributions in Western Australia may be divided into two main types:

1. The southern monospecific meadows of genera with large plants of high biomass, such as *Posidonia* and *Amphibolis*, with small patches of high diversity.
2. The northern mixed seagrass assemblages, extensive on intertidal flats or within reef lagoons or on limestone pavements with sediment veneers.

Distributional limits of tropical and temperate seagrass species occur at different locations along the west coast, *eg* the tropical seagrasses *Thalassia hemprichii* and *Thalassodendron ciliatum* do not occur further south than 22°S, which is also the northern limit for *Amphibolis antarctica*; Shark Bay (26°S) is the southern limit for the tropical species *Cymodocea angustata* (McMillan *et al.* 1983), and *Posidonia australis* has its northern limit here (Walker *et al.* 1988); *Halodule uninervis* and *Halophila spinulosa* have their southern limits at Dongara (29°S) while *Syringodium isoetifolium* extends southwards to Garden Island (32°S). *Posidonia* species do not seem to have temperature related distributional boundaries as most species overlap on the south-west corner of Western Australia, where their distributions seem to be related to habitat availability.

Algal and zoological biogeographers have divided the western coastline into two main provinces, the tropical Dampierian and the temperate Flindersian (Womersley 1982). The boundary line is diffuse for marine algae and seagrasses. More recent analyses of faunal biogeography recognise a Northern Australian Tropical and a Southern Australian Warm Temperate Province with broad zones of overlap on both western and eastern coasts (Morgan & Wells 1991). The Southern Australian Warm Temperate Province, which commences at the Abrolhos Islands, extending southwards and eastwards into the Great Australian Bight, is rich in both overall diversity and species (20 species in 9 genera) and in local diversity, with up to 10 species recorded within 100 m^2 (Kirkman 1985). Despite the wide latitudinal range of the coast, the annual sea temperature range is remarkably small. This is due partly to the Leeuwin Current, which transports warm tropical water southwards in winter, and partly to the absence of any upwelling on the west coast of the continent. This warming may have an effect on seagrass distributions - for example, *Syringodium isoetifolium* extends to Garden Island (32°0'S) on the west coast of Australia but only to Moreton Bay (27°30'S) on the eastern coast.

Setchell (1935) suggested that temperature is the major factor controlling biogeographic distributions in seagrasses, but this hypothesis has been difficult to test around the Australian continent, in the absence of year round temperature data. Although some 'spot' temperatures are available, the information has not been sufficiently comprehensive. Data from loggers positioned on the north-west shelf showed temperature differences of up to 4°C over a tidal cycle, and of at least 2°C between surface and bottom (20 m) (Holloway & Nye 1985, Simpson & Masini 1986). The range of water temperatures is greater in shallow coastal waters than further out to sea, with summer temperatures warmer and winter temperatures cooler near the shore. GOSSTCOMP weekly integrated sea surface temperature profiles (NOAA) have been used to indicate relative temperatures prevailing at different sites, and have been shown at Ningaloo to provide a good correlation with *in situ* mean temperatures (r=.996) (Simpson & Masini 1986).

Comparisons of east and west coast southern limits have been made using these data and those of Rochford (1975, 1984) and Pearce (1986), and are summarised in Table 3. The tropical species *Thalassia hemprichii*, *Thalassodendron ciliatum* and *Halodule uninervis* have different latitudes for their southern limits on the west and east coasts, but have the same winter minimum sea temperature. There is a large difference in the sea temperature at the southern limits for *Halophila decipiens* and *Halophila ovalis* on the east and west coasts but the potential distribution of these plants is limited by the southern extent of land - 35°S on the west coast and 38°S on the east coast. *Syringodium isoetifolium*, *Halophila decipiens* and *Halodule uninervis* all occur further south on the west coast than the east coast.

These examples are all species with tropical affinities which suggests that the most likely influence of the Leeuwin Current on Western Australian seagrass distributions is by extending the southern latitudinal limit of tropical species. The remaining seagrass distributional limits are not correlated with either latitude or temperature. Differences in habitat available for seagrass colonisation on the east and west coasts may explain these distributions. The absence of protected lagoonal systems (potentially another influence of the Leeuwin Current) and of large embayments on the east coast results in most seagrasses being confined to estuaries on the east coast. These environments are more subject to extremes of physico-chemical factors.

One example of the anomalous effect of temperature on seagrass distribution occurs in Shark Bay. Its latitude (26°S) is sub-tropical, yet of the twelve species of seagrass in Shark Bay, the dominant species are of essentially southern distribution at the northern limit of their range *eg Amphibolis antarctica* and *Posidonia australis* (Walker *et al.* 1988). Shark Bay also contains species of tropical affinity such as *Syringodium isoetifolium* and *Halodule uninervis*, but these species occur much further south as well. Biogeographically, the seagrasses in Shark Bay may be regarded as a northern extension of the southern flora. In comparison to adjacent oceanic conditions, water temperatures in Shark Bay are subject to more extreme summer warming and winter cooling, apparent from NOAA imagery (Anderson 1986). The lower winter

Table 3

Biogeographic distribution, latitude of southern limit, winter minimum and summer maximum temperatures for seagrass species on the west and east coasts of Australia

Species	Distribution	Latitude of southern limit (°S)		Temperature (°C)					
				Summer maximum			Winter minimum		
		W	E	W	E	Diff.	W	E	Diff.
Amphibolis antarctica	Southern Australian	35	41	20	17	+3	17	13	+4
Cymodocea angustata	NW Australian Endemic	26	—	24	—		21		
Cymodocea serrulata	Indo-West Pacific	16	28	28	25	+3	24	21	+3
Enhalus acoroides	Indo-West Pacific	16	10	28	30	−2	24	25	-1
Halodule pinifolia	Indo-West Pacific	16	19	28	27	+1	24	22	+2
Halodule uninervis	Indo-West Pacific	26	28	24	25	−1	21	21	0
Halophila decipiens	World-wide in tropics and subtropics	32	38	22	18	+4	18	14	+4
Halophila ovalis	Indo-West Pacific	35	38	20	18	+2	17	14	+3
Halophila ovata	Indo-West Pacific	26	19	24	27	−3	21	22	−1
Halophila spinulosa	NE, W Australia, Indonesia, Malaysia, and Philippines	28	28	24	25	−1	19	20	−1
Posidonia coriacea	SW, S. Australia	35	37	20	19	+1	17	15	+2
Syringodium isoetifolium	Indo-West Pacific	32	28	22	25	−3	18	21	−3
Thalassia hemprichii	Indo-West Pacific	21	19	27	27	0	22	22	0
Thalassodendron ciliatum	Indo-West Pacific	22	20	27	27	0	22	22	0

minimum may allow greater persistence of temperate species, particularly *Amphibolis antarctica*, which releases its viviparous seedlings in winter. These seedlings survive and grow better at lower temperatures (10-15°C) (Walker, unpubl. data 1991).

Contrasts between flora and fauna distributions

Marine invertebrates (Morgan & Wells 1991) and fish (Hutchins 1991) show strong tropical influences, particularly on the west and south sides of Rottnest. In contrast, the algae and seagrasses show much less strong trends. As discussed already, this may be an effect of habitat availability, but it probably also results from a difference in the dispersal mechanisms of the different types of organisms. Unlike animals with planktonic larvae, the propagules of algae are generally much-shorter lived (Suto 1950, Kain 1964) and most settle within a short distance of their source (Hoffman 1987). Van den Hoek (1987) suggested that there is no evidence that there is long distance planktonic dispersal of benthic algal spores, although it may occasionally occur, but that there is more evidence for long-range dispersal by drift algae, particularly for positively buoyant algae such as *Sargassum* and any attached epiphytes. *Sargassum* species are often widely-distributed (Womersley 1987) and, for example, *Sargassum decurrens* occurs at Rottnest Island (32°S) and around the northern Australian coast to Keppel Bay (23°S) in Queensland. This may be a consequence of the southerly flow of the Leeuwin Current. The potential for transport of algal propagules by the Leeuwin Current is reduced in comparison to invertebrate larvae, but there is the potential for algal drift to result in range extensions as a consequence of the Leeuwin Current.

Seagrasses produce seeds or viviparous seedlings which survive longer than algal spores and so have some potential for dispersal. Successful recruitment from these seeds or seedlings, however, is rare on a local scale, as most extension of large temperate seagrass meadows is by vegetative spread (Tomlinson 1974), and there have been no reports of long-distance transport by currents. It is possible that extensions of distribution could occur in a stepped process, but the Leeuwin Current mainly flows well offshore, and may only occasionally touch the coast at different locations. Inshore currents are governed by winds. In summer the southerly influence causes northerly flowing water, while in winter both southerly and northerly flows occur.

The effects of increased winter water temperatures on algal and seagrass survival, productivity and reproductive capacity are completely unstudied. Most coastlines elsewhere in the world have a much larger temperature range, and most species of algae are regarded as being tolerant of a greater range than is found on the Western Australia coastline (van den Hoek 1982). Given the shallow habitats in which they live, and the more extreme fluctuations occurring in these habitats, the potential for the Leeuwin Current to increase the winter minimum is likely to have only a marginal influence on species at the limits of their distribution.

1a. The overall distribution of Indo-West Pacific species - *Syringodium isoetifolioum, Thalassodendron ciliatum, Thalassia hemprichii* and *Enhalus acoroides.*

Fig 1c. Southern Australian species such as *Amphibolis antarctica* and *Posidonia australis.*

Fig 1b The distributions of *Zostera capensis* (▲) and *Heterozostera tasmanica* (•).

Fig 1d *Zostera marina*

Figure 1. Maps of global seagrass distribution. Each map shows the extent of the generalised distribution. For precise distributions of Western Australian species, consult Table 1, for other species, den Hartog (1970) and Phillips & Menez (1988).

Comparisons with South Africa and South America

Both South Africa and South America have extensive subtidal kelp forests particularly on their west coasts, and also have mixed macroalgal assemblages. In South Africa, the combined effects of the Benguela Current and the most intense, clearly defined upwelling in the world result in very cold waters and occasional extreme temperature fluctuations of 10°C in 7 hours (Branch & Branch 1981). Kelp forests of *Ecklonia maxima* and *Laminaria pallida* dominate. The South American coast extends much further south and has extensive forests of *Durvillaea antarctica* and *Lessonia nigrescens* (Santelices *et al.* 1980) in Chile and *Macrocystis integrifolia* and *M. pyrifera* also occur.

Both South Africa and South America show conspicuous absences of seagrasses from their west coasts (Fig. 1). Seagrasses have been recorded from the east coast of Brazil (De Oliveira *et al.* 1983), and there is one record of a small meadow of *Heterozostera tasmanica* from Coquimbo, Chile (30° 16'S) (Phillips *et al.* 1983) and a recent range extension to Caleta Chascos (27°40'S) (Gonzalez & Edding 1990) (Fig. 1b). Aside from this the South American west coast has no seagrass reported over a distance of some 9000 km and, although records are scarce, the habitats are generally unsuitable, again with a rocky shoreline and a relative absence of large sheltered embayments. There are some embayments at high latitudes in Chile, but unlike the extensive Alaskan populations of *Zostera marina,* (Fig. 1d) these southern hemisphere areas are not known to support seagrass meadows.

The Indo-Pacific tropical species are present on the north east coast of Africa (Fig 1a), but decline in species richness and abundance towards South Africa (Phillips & Menez 1988). No seagrass species are reported below about 10°S on the west coast, except *Zostera capensis* which occurs in estuaries around the Cape of Good Hope and up to the mouth of the Orange River (Fig 1b). The west coast of South Africa has not been glaciated and has few large estuaries, although there is extensive sediment movement associated with the Benguela Current, and the Orange River contributes huge amounts of sediment when in flood. The absence of seagrasses would seem to be due mainly to the lack of sheltered habitat.

Conclusions

The effects of the Leeuwin Current on the marine flora of Western Australia are less detectable than its effects on marine animals. Marine macroalgae in south-western Australia have only sporadic occurences of tropical species, with the flora being dominated by southern temperate species. The Leeuwin Current does affect tropical seagrass species in WA by extending their southern latitudinal distribution limits.

The west coast of Western Australia is very different to the east coast of Australia and to the west coasts of South Africa and South America. Macroalgae show similarities between the latter coasts, and are influenced by the prevailing currents and upwellings. The absence of large scale seagrass meadows from both the other west coasts would seem to be a consequence of lack of habitat availability for seagrasses.

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Dispersal of tropical fishes to temperate seas in the southern hemisphere

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Abstract

Western boundary currents in the Southern Hemisphere are capable of dispersing tropical fishes to temperate areas by carrying eggs and larvae from northern breeding grounds in a southerly direction. However, most eastern boundary currents prevent such a dispersal by flowing in the reverse direction, *ie* northwards. An exception to this is the Leeuwin Current, an eastern boundary current which flows southwards along the Western Australian coastline. Furthermore, unlike other south-flowing currents which disperse tropical fishes predominantly during the summer, the Leeuwin Current is involved in an autumn and winter dispersal. This unusual pattern was examined by investigating the temporal and spatial aspects of tropical reef fish recruitment at Rottnest Island (latitude 32°S) in south-western Australia. In addition, this pattern was compared with available data on tropical fish recruitment in other temperate areas of the Southern Hemisphere.

Introduction

The dispersal of tropical marine animals by ocean currents to areas outside their normal breeding ranges is well known, the best documented example involving the Gulf Stream, a western boundary current flowing polewards in the North Atlantic (Randall 1968, Briggs 1974, Thresher 1985). Propagules of animals inhabiting the Caribbean region are picked up by the current and carried northwards along the North American east coast. During the summer, many tropical species are found in sheltered bays in temperate areas, only to disappear with the onset of colder conditions in winter. In the Southern Hemisphere, western boundary currents flowing polewards off South Africa, Australia,and South America, also transport eggs and larvae from tropical breeding grounds southwards to temperate areas during the summer months (Smith 1949, Briggs 1974, Thresher 1985). By contrast, the eastern boundary currents that flow towards the equator in the Southern Hemisphere generally prevent dispersal of tropical forms to temperate areas by flowing in the reverse direction. The exception to this is the Leeuwin Current off south-western Australia, a southward-flowing current originating in waters off north-western Australia (Pearce 1991). This body of warm water provides a vehicle for tropical animals to disperse along the south-western coastline. However, unlike most other poleward-flowing currents, it flows predominantly during the autumn and winter months. During the summer, a northerly flow of cooler water - the West Australian Current - is thought to be the dominant pattern (Maxwell & Cresswell 1981).

For this study, the unusual pattern of a southward-flowing eastern boundary current dispersing tropical species to temperate coasts during the colder months was examined. The investigation was mainly centred on a study of the recruitment of tropical reef fishes at Rottnest Island, Western Australia (latitude 32°S), during the period 1979-1985. As well as examining the spatial and temporal aspects of this recruitment, the degree of persistence of the fauna was also considered. To contrast this situation, information was gathered on, firstly, the summer recruitment of tropical fishes by western boundary currents, in particular the East Australian Current, and secondly, the lack of dispersal of tropical species by the eastern boundary currents off the south-western coasts of Africa and South America.

Leeuwin Current

The occurrence of tropical animals in the littoral fauna of south-western Australia has been known since the early investigations of Saville-Kent (1897) and Michaelsen (1908). Subsequent authors (*eg* Hodgkin & Marsh 1957) suggested that this was related to the presence of a warm, south-flowing current, now known as the Leeuwin Current (Cresswell & Golding 1980). The characteristics of this current are dealt with elsewhere in this publication, but for the purposes of this paper, brief mention of some of its features is necessary. The Leeuwin Current is a stream of warm, low salinity water flowing southwards over the continental shelf in the region of North West Cape (22°S) and Shark Bay (26°S), but moving off the shelf at about 27°S and passing to the west of the Houtman Abrolhos (29°S) and Rottnest Island (32°S). It then rounds Cape Leeuwin (34°S), and flows eastwards across the Great Australian Bight. Satellite imagery and satellite-tracked buoys indicate that the current flows predominantly in autumn and winter, and can reach speeds of between two and three knots (about 80 to 120 kilometres per day) (Pearce 1989).

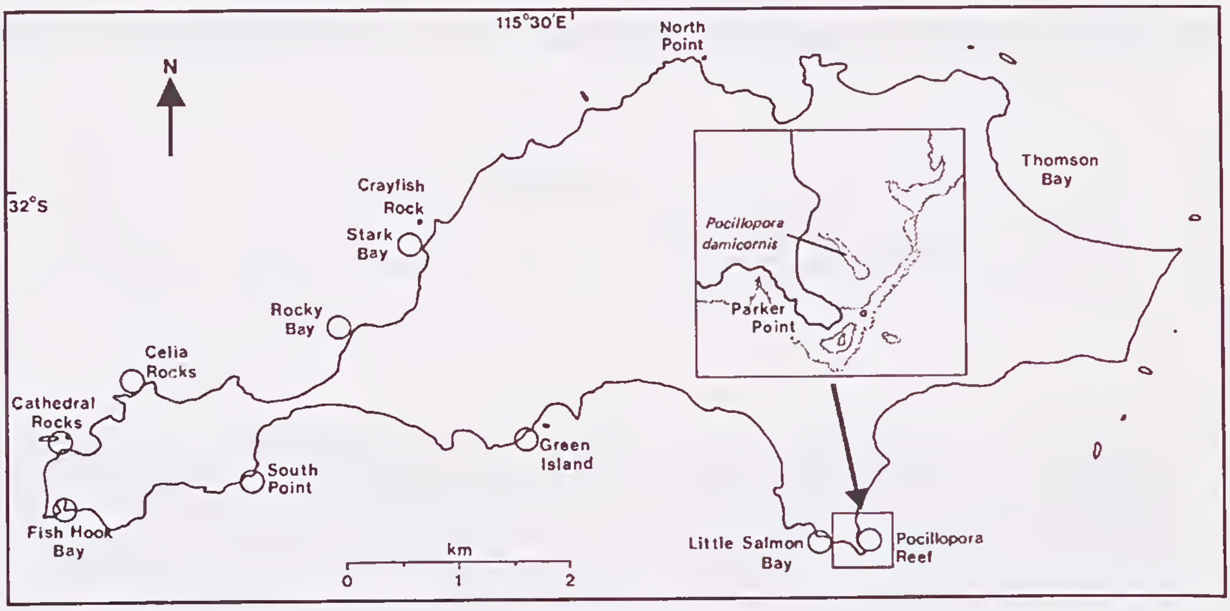

Figure 1 Map of Rottnest Island showing areas of tropical reef fish concentrations (circles). Insert shows an enlargement of the Pocillopora Reef area.

The apparent role played by the Leeuwin Current in the dispersal of tropical fishes along the south-western coastline has been commented on by several authors (Hutchins 1977 & 1979, Maxwell & Cresswell 1981, and Wilson & Allen 1987). There seems little doubt that it is the major contributor to the large size of the transition zone between the temperate and tropical faunas, which ranges from approximately 23° to 35°S. However, the reduction in the numbers of tropical species as latitude increases is more punctuated than gradual. Rottnest Island, at 32°S, is near the southern limit of this transition zone, but nevertheless possesses an unusually rich tropical reef fish fauna. Reefs along the adjacent mainland coast are, by comparison, almost devoid of tropical species. Indeed, the closest inshore reefs to Rottnest Island which enjoy a similar tropical richness are 200 km to the north in the vicinity of Jurien Bay (30°18'S). Is there a connection between Rottnest Island and the Leeuwin Current which may account for this faunal difference?

Rottnest Island is located 18 km off the Western Australian coast, lying close to the edge of the continental shelf. The western portion of the island is bathed by peripheral waters of the Leeuwin Current during autumn and winter (Cresswell & Golding 1980), a feature reflected in the considerably higher minimum water temperatures at the island than in adjacent mainland waters (Hodgkin & Marsh 1957, Hodgkin & Phillips 1969). During the present study, water temperatures taken along the western portion of the island were rarely below 18°C, whereas in mainland coastal waters, the mean minimum was 15°C. The seas of the island are home to a diverse array of fishes best described as belonging to a warm-temperate fauna. However, prominent numbers of tropical species also occur. Of the 360 fishes recorded for the inshore waters of the island, 98 or 27% are tropical species. Of the latter number, 61 species (Table 1) are considered to be either reef dependent or associated with this habitat. In contrast only 11 species of tropical reef fishes have been found in the nearby mainland waters of Perth.

The tropical reef fish fauna of Rottnest Island is concentrated in shallow bays along the western two-thirds of its coastline (Fig. 1); one of these areas is particularly noteworthy. Pocillopora Reef is a shallow lagoon, protected by a prominent headland and a system of seaward reef crests. Its special feature is a 100 m long reef consisting mostly of the coral *Pocillopora damicornis* (see insert, Figure 1). Other smaller colonies of this coral are scattered throughout the lagoon, as well as species of at least five additional coral genera. Reef-dwelling fishes are commonly found in the vicinity of this reef, with smaller numbers in other parts of the lagoon. Large adults of certain species are always present, particularly labrids of the genus *Thalassoma*, but other species have been recorded on the basis of juveniles only. In contrast, the more exposed reefs outside the lagoon support few tropical species, and, in most respects, are generally typical of other temperate reefs in south-western Australia. Nevertheless, some of the deeper reefs around the island are occasionally inhabited by particular tropical fishes which are, at least as adults, rarely seen in these shallow bays.

During autumn, an influx of very small juveniles of tropical fishes occurs on the reefs along the western portion of the island. In the lagoon at Pocillopora Reef, the largest numbers settle either in the shallows at the base of the headland, or in the reef of *Pocillopora damicornis*. This recruitment continues spasmodically throughout the winter, normally ceasing in November (Table 2). In some years, a temporary increase in the numbers settling may occur in October. However, during the period of this investigation, the young of only

Table 1
Tropical reef fishes recorded for south-western Australia

(1 = Rottnest Island; 2 = Perth; 3 = Geographe Bay; 4 = Cape Naturaliste; 5 = Albany; 6 = Recherche Archipelago; j = juvenile; a = adult).

Species	1	2	3	4	5	6
Plotosus lineatus	j,a					j
Antennarius nummifer	j					
Pterois volitans	j,a	a				
Psammoperca waigiensis	a	a				
Epinephelus lanceolatus	a					
Epinephelus rivulatus	a					
Belonepterygion fasciolatum	j					
Plectorhinchus flavomaculatus	a		a			
Plectorhinchus schotaf	a					
Parupeneus chrysopleuron	j,a					
Parupeneus signatus	j,a	j				
Pempheris oualensis	j,a					
Pempheris schwenkii	j					
Platax teira	j,a	j	a	a		
Chaetodon auriga	j,a					
Chaetodon citrinellus	j					
Chaetodon lineolatus	a					
Chaetodon lunula	j,a					
Chaetodon plebeius	j,a					
Abudefduf sexfasciatus	j,a					
Abudefduf sordidus	j					
Abudefduf vaigiensis	j,a					
Plectroglyphidodon leucozonus	j,a					
Pomacentrus coelestis	j					
Pomacentrus milleri	j,a					
Stegastes obreptus	j,a					
Anampses caeruleopunctatus	j					
Anampses geographicus	j,a				a	
Cheilio inermis	a					
Coris aygula	j,a					
Gomphosus varius	j,a					
Hemigymnus faciatus	j					
Labroides dimidiatus	j,a					
Stethojulis bandanensis	j,a					
Stethojulis strigiventer	j,a					
Thalassoma amblycephalum	j					
Thalassoma hardwicke	j					
Thalassoma lunare	j,a					
Thalassoma lutescens	j,a					
Thalassoma purpureum	j,a					
Scarus festivus	a					
Scarus ghobban	j,a					
Scarus gibbus	j					
Scarus reticulatus	j					
Scarus schlegeli	j,a					
Scarus sordidus	j,a					
Entomacrodus striatus	j					
Omobranchus germaini	j,a	j,a				
Petroscirtes breviceps	j	j,a				
Petroscirtes mitratus	j					
Plagiotremus rhinorhynchos	j,a		a		a	
Plagiotremus tapeinosoma	j,a					
Norfolkia brachylepis	j,a					
Amblygobius phalaena	a					
Barbuligobius bohlkei						j
Gnatholepis inconsequens	a					
Priolepis nuchifasciatus		a				
Ptereleotris evides	j					
Acanthurus nigrofuscus	j					
Acanthurus triostegus	j					
Naso unicornis	j					
Siganus fuscescens	j					
Balistoides viridescens	a	a				
Ostacion cubicus		j				
Arothron hispidus		j				
Diodon holacanthus		j				

Table 2
Summary of times of recruitment of 23 species of tropical reef fishes at Rottnest Island

Species	J	F	M	A	M	J	J	A	S	O	N	D
Plotosus lineatus		X										
Parupeneus chrysopleuron					X							
Parupeneus signatus			X	X	X	X		X				
Pempheris oualensis				X		X	X					
Chaetodon plebeius								X				
Abudefduf sexfasciatus			X	X	X	X						
Abudefduf vaigiensis			X	X	X	X				X		
Plectroglyphidodon leucozonus				X								
Stegastes obreptus					X		X					
Anampses geographicus						X	X	X		X		
Labroides dimidiatus					X							
Stethojulis bandanensis							X		X	X		
Stethojulis strigiventer					X							
Thalassoma lunare								X	X	X		
Thalassoma lutescens					X			X		X		
Thalassoma purpureum					X		X	X	X	X		
Scarus ghobban						X	X		X	X		
Scarus gibbus								X				
Ptereleotris evides						X						
Omobranchus germaini	X	X										
Acanthurus nigrofuscus						X						
Acanthurus triostegus			X	X		X				X		
Naso unicornis						X						

one species, the blenny *Omobranchus germaini,* were recruited during the summer months.

The times of settlement for some species were difficult to determine. Although species such as the pomacentrids *Abudefduf vaigiensis* and *A. sexfasciatus* remain in the open after settling, others such as the labrids *Thalassoma purpureum* and *T. lutescens* hide among the rocks and coral and are therefore difficult to detect. Thus, the times of recruitment for some species, as indicated in Table 2, may be affected by this cryptic phase.

Many of the small tropical fish which settle at the Island disappear during the subsequent months, perhaps falling prey to predators, or even succumbing to unfavourable environmental conditions. However, some of the hardier species persist right through the winter months, often surviving to adulthood. These either remain in the shallow bays or move out to deeper offshore reefs as they become larger.

In contrast to the above pattern of recruitment, Russell *et al.* (1977), working on the tropical reef fish fauna at Queensland's One Tree Island (latitude 23°30'S), showed that a peak in recruitment occurs in summer, with most species having a breeding season in the mid spring to early autumn period. They found no evidence of settlement during June and July. This summer peak in recruitment also appears to occur on the coral reefs of Western Australia's northern waters (G R Allen, pers comm). Why is there a difference at Rottnest Island?

As noted earlier, the Leeuwin Current flows predominantly during autumn and winter, weakening and moving away from the island in summer. This close relationship between the commencement and subsequent cessation of tropical recruitment at the island and the arrival and departure of the Leeuwin Current indicates that this current is obviously carrying the young of these tropical fish species to Rottnest Island. The two peaks of recruitment possibly involve larvae from the end of one northern breeding season (late summer - early autumn) and the beginning of the next (mid spring). (Evidence provided by satellite imagery does show that in some years the Leeuwin Current is still present in the Rottnest Island area during October). Individuals recruited during the winter months may include late arrivals at the island which have been temporarily trapped in isolated eddies of the current. Furthermore, the lack of new recruits in summer suggests that tropical reef fishes are not breeding at Rottnest Island. As mentioned earlier, the only exception to this is the blenny *Omobranchus germaini*, a hardy inhabitant of shallow reef flats and intertidal areas which is able to tolerate a considerable range of environmental conditions. It is widespread at the island and is also one of the few tropical reef fishes which is reasonably numerous on the coastal reefs of the nearby mainland.

The most likely source of breeding stocks to the north of Rottnest Island is the Houtman Abrolhos, an area also in the path of the Leeuwin Current. Although a considerable distance south of the tropics, many of the tropical reef fishes at the Houtman Abrolhos appear to be breeding successfully (G R Allen, pers comm); this includes most of those tropical species recorded for Rottnest Island. The latter all have pelagic larvae which are capable of surviving in the plankton for moderate periods (*eg* larval durations of between 39 and 55 days for *Thalassoma lunare* and 19 to 27 days for *Abudefduf vaigiensis* are given by Victor 1986 and

Thresher *et al.* 1989, respectively). This should easily be enough time for the planktonic larvae to cover the 350 km between the Houtman Abrolhos and Rottnest Island at a current rate as high as 2-3 knots, even allowing for breaks in southwards movement due to meanders and eddy formation, etc.

South of Rottnest Island, records of tropical reef fishes are spasmodic and widespread (Table 1), with two species being found as far east as the Recherche Archipelago. The report of *Epinephelus lanceolatus* from the Coorong in south-eastern South Australia by Kailola & Jones (1981) indicates the great distances that can be covered by current-borne tropical larvae. Nevertheless recruitment success for tropical reef fishes in these more southern areas appears to be poor.

Therefore, the connection between Rottnest Island and the tropical richness of its fauna is primarily the offshore location of the island and the influence of the Leeuwin Current. This current flows well offshore from mainland reefs and other inshore islands, but bathes the western portion of Rottnest Island. Not only does the current carry the propagules of tropical reef fishes to the island, but it also maintains relatively high water temperatures during the winter. In addition, Rottnest Island provides numerous protected habitats which are conducive to settlement by tropical larvae. The corals in these areas obviously provide the shelter and food preferred by them. Some tropical species probably reach mainland reefs in the wind-blown upper surface layers of the water column, but only the very hardiest of species survive the less favourable inshore conditions.

East Australian Current

The presence of significant numbers of tropical reef fishes in south-eastern Australia during summer has long been an attraction for recreational divers and aquariasts (Lawler 1984, Fallu 1985). Although a relatively rich tropical fauna occurs all year round on the reefs of northern New South Wales (approx. 30°S), this fauna gradually diminishes as the latitude increases, becoming more of a seasonal phenomenon in central New South Wales (approx. 33°S), and eventually disappearing in the region of the Victorian border (latitude 37°30'S). Nevertheless some localities near the southern extremity of this range possess prominent numbers of tropical fishes during the summer months. An unpublished report (Kuiter 1981) on the fishes of Montague Island (36°15'S) listed 75 species of tropical reef fishes, and a survey by the present author in 1981 at the nearby mainland locality of Merimbula (37°S) produced 50 species. The latter investigation involved a study of the recruitment of tropical reef fishes near the entrance to Merimbula Lake. Here, the recruitment of tropical fishes commences in late November or early December, and continues until about April. These times coincide with the southwards movement of the East Australian Current, which brings warmer tropical waters down the eastern Australian coast to Bass Strait, mainly in summer (Rochford 1984). In autumn the current moves away from the coast and tropical recruitment ceases. With the onset of unfavourable environmental conditions in winter, most individuals of these tropical species disappear during May and June. At Montague Island, however, a few of the hardier species (*eg* the scorpaenid *Pterois volitans*) may persist throughout the winter, especially when water temperatures remain higher than normal (Kuiter 1981).

Comparing the dispersal of tropical reef fishes between south-eastern and south-western Australia, temporal and spatial differences are obvious. In south-eastern Australia, recruitment takes place mostly during the summer months, with significant numbers of recruits being found as far south as latitude 37°S, whereas in south-western Australia, recruitment is more of a late autumn to winter phenomenon and virtually ceases at latitude 32°S. This can be best explained by the seasonal differences in flow of the respective currents. The summer-flowing East Australian Current transports its larvae southwards during a period of rising water temperatures, so settlement occurs when conditions are more favourable. In contrast, the Leeuwin Current transports larvae during times when water temperatures are falling, and therefore, only the hardiest are likely to survive. In addition, more propagules of tropical fishes - which generally breed during the warmer months - would be available to a summer- flowing current than a winter-flowing one.

Southern Africa

The Agulhas Current transports propagules of tropical reef fishes to temperate areas of South Africa in summer (Penrith 1976, Beckley 1985). This dispersal occurs regularly to Algoa Bay (34°S) but occasionally such transients are found in the vicinity of the Cape of Good Hope (Beckley *et al.* 1987). Generally they do not survive to adulthood in these higher latitudes, gradually disappearing with the onset of winter (Beckley 1985). Many of these tropical species are the same species also being dispersed to temperate waters of south-eastern and south-western Australia (Beckley *et al.* 1987).

Tongues of the Agulhas Current can also be found off the lower west coast as isolated eddies entrapped in the cold north-flowing Benguela Current (Penrith 1976, Shannon & Agenbag 1987). However, any larvae originating from the tropical east coast carried by these eddies would be unlikely to settle given the unsuitable environment for reef fishes along the exposed sandy coasts of south-western Africa (Penrith 1976). Furthermore the cold conditions resulting from a combination of the Benguela Current and seasonal cold water upwelling would prevent survival.

Species of reef fishes originating from tropical west Africa are rare in south-west Africa, given the absence of a south-flowing current and the presence of large expanses of sandy coast between the Orange River (29°S) and southern Angola (17°S) (Penrith 1976).

South America

Little has been published on the dispersal of tropical reef fishes in temperate areas of South America. However, on the west coast, the combination of upwelling and the cold north-flowing Humboldt Current would obviously restrict the southward movement of tropical forms. Briggs (1974) indicated that the influence of these conditions has pushed the southern limit of the tropical fauna almost to the equator. On the eastern side, the warm Brazil Current flows almost as far south as the waters off the Rio de la Plata (35°S) where it meets the cold north-flowing Falkland Current. Briggs (1974) stated that the Brazil Current maintains a tropical fauna to at least Rio de Janeiro (23°S).

Therefore, it could be expected that the dispersal of tropical reef fishes by this current should continue well into the warm temperate regions of Brazil.

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Mass spawning of corals on Western Australian reefs and comparisons with the Great Barrier Reef

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Abstract

Multispecific, synchronous spawning or 'mass spawning' of scleractinian corals on Western Australian reefs was observed fortuitously in the Dampier Archipelago in March 1984. Subsequent studies during 1985-1988 have documented this phenomenon along the Western Australian coastline on tropical and temperate coral reefs and spawning has been observed to occur simultaneously on reefs separated by over 12 degrees of latitude. Mass spawning occurred mainly around the third quarter of the moon (*ie* 7-9 nights after the full moon) on neap, nocturnal, ebb tides. Although most of the corals studied spawned after the full moon in March each year, in some years, some spawned on the same nights after the full moon in April. Studies since 1988 have shown that a small percentage of corals spawn after the full moons in February and April each year.

As a result of these studies, 102 species of scleractinian corals from Western Australian reefs are now known to spawn during the austral autumn. A further 44 species were found to contain ripe gonads during the same period and are presumed to participate in the annual coral mass spawning on Western Australian reefs. These records represent 88% of the coral species studied so far or about 46% of the coral species currently described from Western Australia.

In Western Australia, coral mass spawning coincides approximately with the annual intensification of the Leeuwin Current, a warm poleward current of tropical origin that flows unidirectionally along the coastline of Western Australia during the austral autumn and winter. This current provides a mechanism for the southward dispersal of planulae and raises the possibility of a unidirectional gene flow between regionally separate coral reefs in Western Australia.

Comparisons with the spring coral mass spawnings on the Great Barrier Reef indicate that, apart from the seasonal difference in the timing of spawning, many similarities exist suggesting that the same phenomenon is occurring on both sides of Australia. Comparisons of annual sea temperature patterns however, both within Western Australia and between the east and west coasts of tropical Australia, suggest that sea temperature is not a proximate or ultimate factor in determining the breeding season of scleractinian corals. It is postulated that the different seasonal timing of coral mass spawning on the east and west coasts of Australia is the result of an endogenous rhythm reflecting the breeding patterns of ancestral corals as a consequence of selective dispersal of larvae from equatorial regions.

The simultaneous spawning of many other coral reef invertebrates during the coral mass spawnings suggests that the findings presented here in relation to scleractinian corals have important implications regarding the reproductive patterns of many other coral reef animals.

Introduction

The recent discovery of multispecific, synchronous spawning or 'mass spawning' of tropical reef corals on the Great Barrier Reef and on Western Australian reefs has greatly increased our understanding of the reproductive patterns of many scleractinian corals (Harrison *et al.* 1983, Harrison *et al.* 1984, Simpson 1985, 1987, Babcock *et al.* 1986). In contrast to the brief, predictable spawning periods of corals on the Great Barrier Reef and on Western Australian reefs, corals in the Red Sea exhibit temporal reproductive isolation (Shlesinger & Loya 1985) indicating that the reproductive traits of reef corals are highly variable. The proximate (environmental) and ultimate (ecological) factors responsible for these reproductive patterns are poorly understood. As pointed out by Willis *et al.* (1985), comparisons of the reproductive patterns of corals between geographic regions may

identify common factors that will possibly pinpoint underlying causes of the mass spawning phenomenon.

Following the fortuitous discovery of coral mass spawning in the Dampier Archipelago (Fig. 1) during March 1984, studies at the same location in 1985 confirmed that coral mass spawning occurred during a brief predictable period after the full moon in March. The coral species involved were documented and aspects of the physical environment during the spawning period were characterised (Simpson 1985). Similar studies at the Dampier Archipelago and the Ningaloo Reef in 1986 confirmed that coral spawning at these two locations occurred synchronously, and studies at the Abrolhos Islands in March 1987 determined that coral mass spawning on these temperate reefs occurred at approximately the same time as on tropical reefs in Western Australia (Simpson & Masini 1986, Simpson 1987). In addition, volunteer observers were stationed along the coastline of Western Australia in March 1987 and 1988 to determine the extent of coral spawning synchrony within and between regionally separate coral reefs in Western Australia (Simpson 1988).

In this paper I summarise the results of coral mass spawning studies on Western Australian reefs between 1985 and 1988 and draw comparisons with the spring mass spawnings on the Great Barrier Reef. An hypothesis explaining the difference in the seasonal timing of the breeding seasons of scleractinian corals on the east and west coasts of Australia is also outlined.

Methods

Polyp reproductive status was determined by the presence of pigmented eggs either by examination of freshly broken pieces of live coral in the field or under a dissecting microscope in the laboratory. In addition to ripe eggs, the presence of testes and motile sperm with condensed heads were used as criteria for reproductive maturity (Harrison *et al.* 1984). Spawning of corals in the field was determined directly by observation of gamete release *in situ*, the appearance of eggs on the sea surface, or inferred from the disappearance of mature gametes in sequential samples from tagged colonies.

In most years 200+ coral colonies were tagged in the two weeks before the predicted time of spawning and their reproductive status was determined by the methods outlined above. The reproductive status of a representative subset of these colonies, usually numbering about 30-50, was monitored daily. Random collections were also made during the week before and after spawning. Untagged species observed to be spawning during night dives were also recorded or collected. In general, night observations were carried out between sunset and about 2230 h on about 6 nights around the time of predicted spawning, usually 6-11 nights after the full moon. In earlier years searches for coral eggs floating on the sea were made on several nights either side of these dates, usually between sunset and 2100 h. These combined observations, together with the daily monitoring of tagged colonies, ensured that spawning dates were determined accurately.

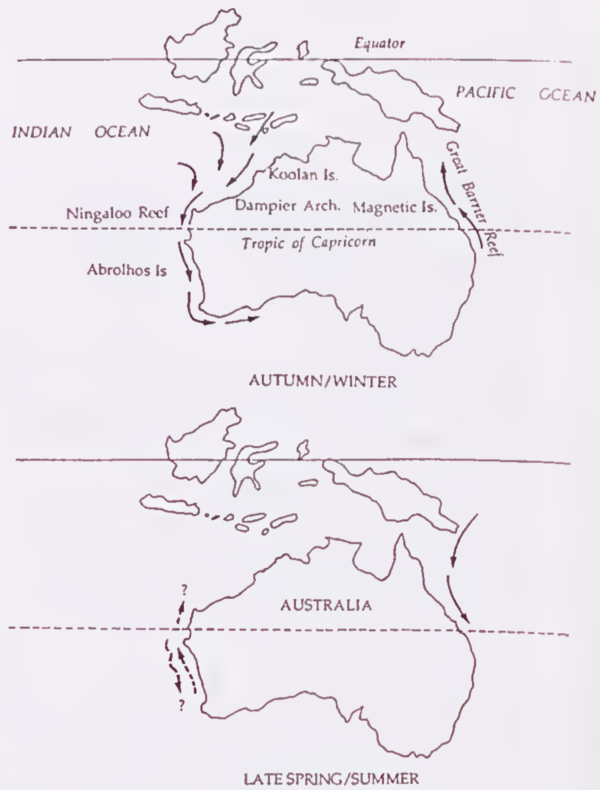

Figure 1 Seasonal variation in the drift of surface waters on the east and west coasts of Australia. The change from a variable or northerly drift to a net southerly drift occurs around March on the west coast and around November on the east coast and coincides approximately with the timing of coral mass spawning at both locations.

Details of the species and number of colonies that were sampled in the Dampier Archipelago in November 1984 and March 1985 can be found in Simpson (1985). In 1986, 512 colonies from at least 74 species were sampled at the Dampier Archipelago and the Ningaloo Reef (Simpson, unpublished data). In 1987, 422 colonies from 107 species were sampled from the Abrolhos Islands (Babcock *et al.* unpublished data). In 1988, 387 colonies from at least 51 species were sampled from Ningaloo Reef. As a result of these surveys, most of the coral species that were studied were sampled repeatedly at two or all of these locations.

Table 1

Summary of coral mass spawning observations on Western Australian Reefs during March 1987. Sea temperatures are monthly means from Pearce (1986); tidal data from Easton (1970). (s, semi-diurnal tides; d, mainly diurnal tides; * estimated tide and temperature data).

Location	Latitude (°S)	Tide range (m)	Temperature range (°C)	Dates of main spawning	Nights after full moon
Koolan Is.	16	>10/s	31-24	23, 24	8, 9
Dampier Arch.	20	~5/s	30-22	23, 24	8, 9
Lowendal Is.*	20	~4/s	30-23	23, 24	8, 9
Ningaloo Reef	23	<2/s	27-23	23, 24	8, 9
Abrolhos Is.	28-29	~1/d	24-20	25, 26	10, 11

Results

Preliminary studies of coral gametogenesis, the results of tagging studies and random surveys in the weeks before and after spawning, as well as direct observations, indicate that most of the corals studied spawned after the full moon in March each year. During some years, however, a small percentage of corals with ripe gonads did not spawn after the March full moon (Simpson 1985). Observations of a small number (<10) of colonies spawning and a small spawn slick at Coral Bay (M Forde, pers. comm) after the full moon in April in 1986 suggest that these corals spawn a month later. Further observations since 1988 indicate that a small percentage of corals (usually less than 10%) spawn after the full moons in February and April each year.

Spawning occurred mainly around 7-9 nights after the full moon during a period of maximum sea temperatures, within 3-4 hours after dark and during neap, ebb tides (Simpson 1985, 1987, 1988). An exception occurred in 1987 at the Abrolhos Islands where spawning occurred mainly on the 10th and 11th nights after the full moon. Direct observations and results from daily monitoring of tagged corals indicated that, in most years, a small percentage of the coral population spawned on one or two nights either side of the main spawning nights (Simpson, unpublished data). Simultaneous observations along the coastline of Western Australia in March 1987 indicated that a high degree of spawning synchrony exists within and between regionally separate coral reefs in Western Australia, and that spawning on these reefs occurred under markedly different environmental conditions (Table 1). Similar observations in 1988 support these conclusions (Simpson 1987).

A total of at least 165 species of scleractinian corals (41 genera, 13 families) were examined in the periods following the full moon in March between 1985-1988 (Table 2). These studies indicate that at least 102 species of corals that occur on Western Australian reefs shed gametes during a brief, predictable spawning period each year. A further 44 species contained ripe gonads, indicating that spawning was imminent and suggesting that these species also participate in the mass spawning. The total of definite and probable spawning species represents approximately 46% of the 318 species of scleractinian corals, from 70 genera, currently described from Western Australia (Veron & Marsh 1988). A high percentage (88 %) of the coral species that were examined were either definite or probable spawners suggesting that many of the other unexamined coral species that occur on Western Australian reefs are likely to be involved in the annual mass spawning event.

None of the coral species that were examined contained or released planulae during this period and mature gonads were not observed in any corals collected during November 1984 or May to October 1985. In addition, preliminary data on the gametogenic cycle of species of Acroporidae, Faviidae, Mussidae and Oculinidae at Ningaloo Reef between 3 October 1985 and 26 March 1986 suggest that the gametogenic cycles of these species are similar to the same or like species on the Great Barrier Reef (Marshall & Stephenson 1933, Kojis & Quinn 1981, Harriot 1983, Babcock 1984, Wallace 1985) although it is offset by 4-5 months.

Table 2.

Comparison of the number of coral species found to be definite or probable autumn spawners on Western Australian reefs in relation to the total number of species currently known from Western Australia (* from Veron & Marsh 1988) and the number of species examined.

FAMILY	Number of species in Western Australia*	Number of species examined	Number of species that spawned	Number of species with ripe gonads
ASTROCOENIIDAE	2	1	0	0
POCILLOPORIDAE	9	1	0	0
ACROPORIDAE	98	60	50	7
PORITIDAE	30	16	6	7
SIDERASTREIDAE	12	5	0	2
AGARICIIDAE	20	7	1	3
FUNGIIDAE	28	4	1	3
OCULINIDAE	3	2	1	1
PECTINIDAE	11	6	4	2
MUSSIDAE	17	8	4	3
MERULINIDAE	7	6	2	3
FAVIIDAE	59	42	30	9
TRACHYPHYLLIIDAE	2	0	-	-
CARYOPHYLLIIDAE	9	1	1	-
DENDROPHYLLIIDAE	11	6	2	4
TOTAL	318	165	102	44

Reproductive swarmings of polychaete worms, predominantly rag-worms (Polychaeta: Nereidae) but including many other species such as *Eunice* cf *australis*, occurred simultaneously with the coral mass spawnings in all instances. The epitokous (reproductive) stage of these worms emerged following the onset of coral spawning. Other taxa observed spawning during this period include Alcyonarians and species of Mollusca and Echinodermata (Marsh 1988).

Discussion

There are many similarities between the coral mass spawning events observed on the Great Barrier Reef and on Western Australian reefs. Most species are simultaneous hermaphrodites and spawn after a full moon, over 2 or 3 consecutive nights, during a period of neap tides and within 3 to 4 hours after sunset. Additionally, mass spawning appears to be a predictable, annual event in both locations and approximately 60% of the species observed to spawn or contain ripe gonads in Western Australia mass spawn on the Great Barrier Reef (Harrison *et al.* 1984, Babcock *et al.* 1986, Shlesinger & Loya 1985, Simpson 1985, 1986). The colours, general buoyancy (Babcock *et al.* 1986) and size range of mature eggs (Marshall & Stephenson 1933, Kojis & Quinn 1981, Harriot 1983, Babcock 1984, Wallace 1985) and the most common spawning behaviour are also similar (Babcock *et al.* 1986). The synchronous spawning of corals on regionally separate reefs (Table 1, Babcock *et al.* 1986) and the time between consecutive spring spawnings on the Great Barrier Reef and autumn spawnings on Western Australian reefs (Willis *et al.* 1985, Babcock *et al.* 1986, Simpson 1988) are further similarities. The remarkable likeness of coral spawning on the east and west coasts of Australia suggests that the same phenomenon is being observed.

Different seasonal timing of mass spawning, and as a consequence, the different environmental conditions that exist during the periods of gametogenesis, spawning, larval development and settlement are the most significant differences between the two locations. For example, mass spawning on the Great Barrier Reef occurs after a period of rapidly rising sea temperatures, although these temperatures are still well below the maxima for these locations (Fig. 2a). In contrast, spawning on Western Australian reefs coincides with the period of maximum seawater temperatures (Fig. 2a, b). There are further differences. Corals on offshore reefs in tropical Western Australia (*eg* Lowendal Is) spawn at the same time as corals on inshore reefs (*eg* Dampier Archipelago, Table 1), in contrast to the one month difference that occurs between Magnetic Island and the offshore reefs on the Great Barrier Reef (Babcock *et al.* 1986). Corals on the Great Barrier Reef also spawn around neap tides but, because of the aphasic tides in tropical east Australia, spawning occurs mainly three to six nights after the full moon. As a result, spawning on the Great Barrier Reef occurs before, during and after moonrise (Babcock *et al.* 1986) whereas in Western Australia, corals spawn well before moonrise (Simpson 1985). A further difference is that species of *Turbinaria* participate in the mass spawning

mainly three to six nights after the full moon. As a result, spawning on the Great Barrier Reef occurs before, during and after moonrise (Babcock *et al.* 1986) whereas in Western Australia, corals spawn well before moonrise (Simpson 1985). A further difference is that species of *Turbinaria* participate in the mass spawning event in Western Australia but not on the Great Barrier Reef where spawning of this genus occurs in autumn (Harrison *et al.* 1984). These differences possibly reflect adaptation to local conditions.

Coral mass spawning on Western Australian reefs coincides approximately with the annual intensification of the Leeuwin Current, a warm poleward current of tropical origin that flows unidirectionally along the Western Australian coastline in autumn and winter (Cresswell & Golding 1980, Godfrey & Ridgway 1985). This current flows predominantly, but not exclusively, during the austral autumn and winter and provides a mechanism for the southward dispersal of coral planulae which, in turn, raises the possibility of a unidirectional gene flow between regionally separate coral reefs in Western Australia.

The reproductive cycles of marine invertebrates are considered to be influenced predominantly by temperature (Orton 1920, Giese & Pearse 1974) and this factor has been suggested as having an important influence in timing the gametogenic cycle of scleractinian corals (Harrison *et al.* 1984, Babcock *et al.* 1986, Oliver *et al.* 1988, Richmond & Hunter 1990). Furthermore, differences in temperature patterns have been suggested as possible explanations for observed differences in the timing of coral spawning on the northern (Harriot 1983) and southern (Kojis & Quinn 1981) Great Barrier Reef and between the onshore and offshore reefs on the central Great Barrier Reef (Babcock *et al.* 1986). Seawater temperatures at the Dampier Archipelago show a pronounced seasonal pattern and are similar to sea temperatures at Magnetic Island, yet the breeding seasons of corals at these two locations are about 5 months apart (Fig. 2a). In contrast, sea temperature patterns along the Western Australian coastline are quantitatively and qualitatively different due to the varying influence of the Leeuwin Current, yet mass spawning occurs synchronously between regionally separate reefs (Fig. 2b, Table 1) and between onshore and offshore reefs (Table 1). These data suggest that sea temperature is not a universal proximate cue or ultimate factor in determining the timing of the breeding season of scleractinian corals.

An alternative hypothesis is that the breeding season of corals in Australia is not controlled by environmental cues but is the result of an endogenous rhythm which reflects historical breeding patterns of ancestral corals (Simpson 1987, 1988) and has been termed the Genetic Legacy Hypothesis by Oliver *et al.* (1988). Ocean circulation patterns at the time of coral spawning on the east and west coasts of Australia and preliminary data on the breeding season of corals in equatorial regions support this hypothesis. Mass spawning of corals occurs in late spring/early summer on the Great Barrier Reef and during autumn on Western Australian reefs. In both locations spawning coincides approximately with the annual change from a northerly or variable net drift to a pronounced net southerly drift of surface waters (Fig. 1) and with periods of calms associated with the seasonal changes in monsoonal wind patterns (Pickard *et al*, 1977, Williams *et al.* 1984, Holloway & Nye 1985). The southerly drift of tropical water along the Great Barrier Reef originates from the South Equatorial Current and occurs during late spring and summer whereas during autumn and winter surface waters of the Great Barrier Reef drift northward under the influence of the south-east trade winds. Off Western Australia the opposite situation exists. The Leeuwin Current, originating as inflow from the Western Pacific to the Indian Ocean through the Indonesian Archipelago (Godfrey & Ridgway 1985), flows strongly southward along the coastline during autumn and winter. Weaker flows and periodic reversals occur during late spring and summer when south-westerly winds predominate. Thus, in both areas, albeit in different seasons, a mechanism exists for the southward transport of coral larvae from equatorial regions.

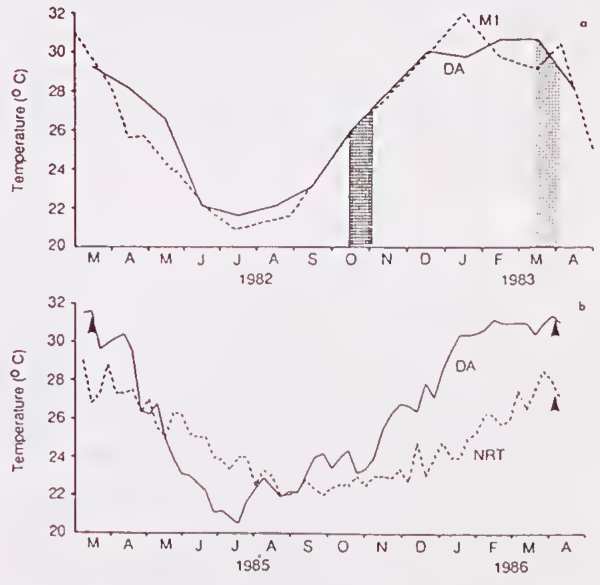

Figure 2 (a) Annual seawater temperature patterns and asynchronous breeding seasons of corals at Magnetic Island (MI, dark shade) and the Dampier Archipelago (DA, light shade); (b) annual seawater temperature patterns and synchronous periods of coral mass spawning (arrows) at the Dampier Archipelago (DA) and the Ningaloo Reef tract (NRT). Data for the Dampier Archipelago for (a) from monthly means and (b) from weekly means. Data for Magnetic Island from Babcock *et al.* (1986) and for the Ningaloo Reef from weekly means.

Preliminary studies of coral reproduction in equatorial regions have shown that the breeding season of several coral species extends from approximately September to March (Oliver *et al.* 1988). The same species are known to spawn in spring on the Great Barrier Reef and in autumn on Western Australian reefs. Thus as a result of this extended breeding season and the seasonal difference in the flow of tropical water down the east and west coasts of Australia, coral larvae produced in equatorial regions during the austral spring and summer are more likely to be transported to the east coast of Australia than to the west coast. Similarly, larvae produced in equatorial regions during the austral autumn are more likely to be transported to the west coast of Australia than the east coast. If this is the case, the different spawning seasons of corals on the east and west coasts of Australia may well be a reflection of ancestral breeding patterns and be the result of selective dispersal of coral larvae from equatorial populations that have extended breeding seasons. However, as Oliver *et al.* (1988) point out, this hypothesis would be weakened if corals from equatorial regions spawned more than once a year. Although their study in Papua New Guinea indicated that some individual corals had ripe gonads in September-November and January-March, suggesting two gametogenic cycles and, therefore two spawning periods, this has yet to be proven specifically or generally. A common origin would explain the remarkable similarity in many of the reproductive traits observed in corals on the east and west coasts of Australia. Furthermore, an endogenous rhythm would also explain the latitudinal synchrony of coral spawning on reefs with markedly different environmental conditions (Table 1).

Within the breeding season, corals on the east and west coasts of Australia appear to respond to lunar/tidal patterns and light/dark cycles as proximate cues for spawning synchrony (Babcock *et al.* 1986, Simpson 1988). The variation in the time of spawning within the respective breeding seasons on the east and west coasts of Australia (*eg* different nights after the full moon), is probably the result of local adaptation.

At present the mass spawning of scleractinian corals has been recorded only on the east and west coasts of Australia. Mass spawning does not appear to occur in the Caribbean Sea (Szmant-Froelich *et al.* 1984) or in the Red Sea (Shlesinger & Loya 1985). A suggested explanation is that environmental conditions at these locations are less extreme than on the Great Barrier Reef (Shlesinger & Loya 1985). The data presented here suggest this is not the case, as tides and sea temperatures vary markedly, both qualitatively and quantitatively, along the Western Australian coastline yet mass spawning occurs synchronously. In contrast, tides and sea temperatures at Magnetic Island and at the Dampier Archipelago are similar yet mass spawning is about 5 months out of phase. Why corals exhibit reproductive traits as diverse as temporal reproductive isolation and synchronous multispecific spawning is not clear. Perhaps the reproductive patterns of Red Sea corals are indeed adaptations to an unstable environment that has occurred throughout their evolutionary history (Shlesinger & Loya 1985) or perhaps it is merely a reflection of their 'diffuse' origin. The similarity of coral mass spawning on the east and west coasts of Australia suggests that multispecific, synchronous spawning during brief, annual periods may be a common reproductive pattern for reef corals. Whether this reproductive pattern is confined to non-equatorial coral populations that are genetically 'connected' to equatorial coral populations by ocean currents remains to be seen.

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The Leeuwin Current and larval recruitment to the rock (spiny) lobster fishery off Western Australia

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Abstract

The phyllosoma larval stages of the western rock lobster (*Panulirus cygnus*) spend almost a year drifting in the south-eastern Indian Ocean, before metamorphosing to the puerulus stage and returning to the shelf. The pueruli settle in the coastal reefs where the juveniles remain for a period of three to five years and then recruit to the fishery.

Although previous studies have shown that there is a clear link between the Leeuwin Current and larval (puerulus) recruitment, the mechanisms which act on the larval stages or pueruli to bring this about are as yet unknown. This study of monthly larval settlement and environmental factors over the geographical range of the fishery between 1984 to 1989 shows that settlement along the coast of Western Australia follows a similar seasonal pattern at all sites and that there is a close correlation between adjacent sites. However, not all sites receive puerulus settlement annually, especially in the southern area of the fishery.

Cross correlation of Southern Oscillation Index, sealevel, sea surface temperature and salinity, with puerulus settlement at all sites indicates that similar processes are affecting larval recruitment along the whole coast. Comparison with a long series of data for a 20 year period from the central area of the fishery indicates that the correlations with sealevel from the 5-year data set are valid.

Introduction

The catch of the western rock lobster (*Panulirus cygnus* George) fishery off Western Australia (Fig. 1) is largely taken between latitudes 28 and 32°S and has an annual value of about $A200 million.

There are two distinct aspects of interest in recruitment to the fishery: the link between larval settlement and recruitment, and the factors responsible for variations in the level of puerulus settlement. First, the prediction of recruitment to the fishery is based on the demonstration that the commercial catch off Western Australia in any year is highly correlated with the level of puerulus settlement four years previously (Morgan *et al.* 1982, Phillips 1986). Second, the mechanisms contributing to the level of settlement need to be determined. There is, for example, a link between settlement and interannual variability in the flow of the Leeuwin Current, the anomalous poleward boundary current in the southeastern Indian Ocean (Pearce & Phillips 1988). However, the physical mechanism(s) responsible for the fluctuating levels of settlement are as yet unknown.

Current research by CSIRO is aimed at the second aspect, specifically a better understanding of the relationships between oceanic processes and the larval settlement in the coastal reefs as pueruli. This paper examines the results of a five year study of the spatial and temporal variability of puerulus settlement and environmental conditions over the geographic range of the fishery.

Oceanic Part of Life Cycle

The life cycle of *P. cygnus* includes a nine to eleven month period in the southeast Indian Ocean. The larvae, which are flat and leaflike in shape, called phyllosoma, hatch in late spring or summer from females present on the outer edge of the continental shelf. They are transported out into the ocean, some of them up to 1500 km (Phillips 1981). The larvae remain at the phyllosoma stages for nine to eleven months during autumn and winter, increasing in size as they moult. At least nine phyllosoma stages are recognisable.

In late winter and early spring, the last phyllosoma stage transforms to a puerulus stage, which completes the oceanic cycle by swimming across the continental shelf and settling in the shallow limestone reef areas along the coast (Phillips *et al.* 1979, Phillips 1981). The settled puerulus stage moults into a small juvenile rock lobster. The peak settlement of pueruli occurs between September and January, following hatching in the previous November to February periods (Phillips *et al.* 1979).

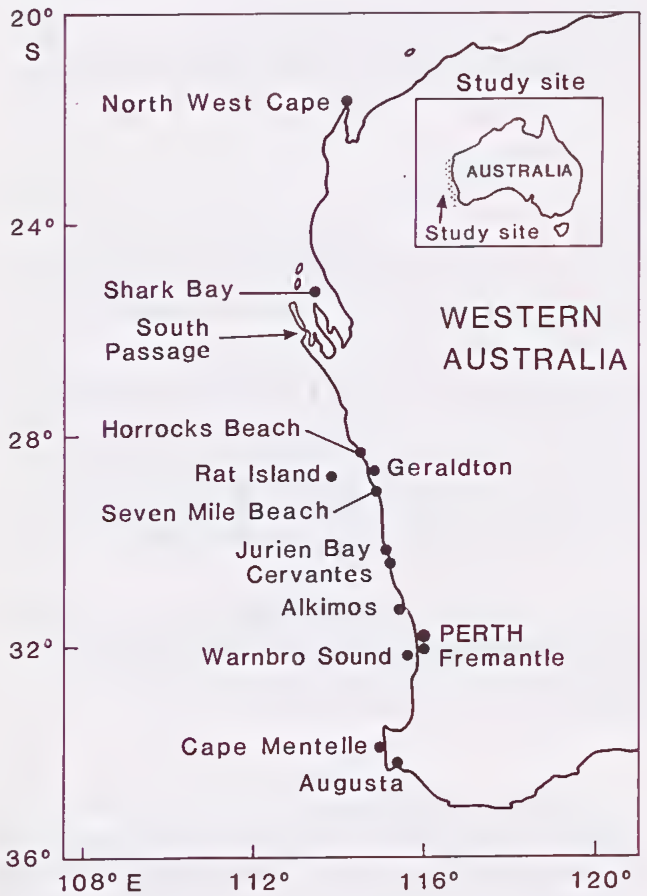

Figure 1 Map of Western Australia showing the sites at which the puerulus stage of *Panulirus cygnus* were sampled.

The Leeuwin Current

In autumn, winter and (to some extent) spring, the Leeuwin Current is evident in satellite imagery as a band of warm water sweeping southwards down the West Australian continental margin, around Cape Leeuwin and into the Great Australian Bight (Prata *et al.* 1986). In summer, by contrast, the flow is apparently much weaker. However, the satellite data show quite clearly that there is still a southwards-flowing stream during the summer months, so that there is a net southwards flow through the period of puerulus settlement between August and February, albeit with intermittent periods of northwards currents especially near the coast (Boland *et al.* 1988).

The satellite imagery has also shown that the Leeuwin Current is a complex of jets, meanders and eddies. The meanders transport warm water some 100 km or more into the Indian Ocean, and then back towards the coast. Current measurements using satellite tracked buoys indicate that onshore current jets associated with these meanders can exceed 150 cm s^{-1} or 3 knots (Pearce & Phillips 1992). Any phyllosomata entrained into this eastwards flow would be carried towards the shelf, where the transformation to puerulus and consequent settlement would presumably occur. Such oceanic features are often strongest in winter and early spring (at the start of the settlement period), perhaps providing one possible mechanism for returning pueruli to the shelf. Apart from these offshore features, the inshore boundary of the Current sometimes washes onto the shelf and brings warm Leeuwin Current water inshore, again possibly contributing to the settlement process. This may apply particularly in the southern areas because of the narrowness of the shelf.

Although the Leeuwin Current is a strong flow towards the south along the outer shelf and slope, currents along the central and inner shelf tend to reverse between northward and southward with a period of a few days (Cresswell *et al.* 1989). The mean drift is northwards at about 10 cm s^{-1} in summer and southwards at 20 cm s^{-1} in winter, but the oscillating currents can reach 50 cm s^{-1} (1 knot).

The Data

Puerulus

Phillips (1972) showed that the puerulus stage of *P. cygnus* can be captured with collectors composed of artificial seaweed moored at the surface within the protection of the coastal reefs. Subsequently, Phillips & Hall (1978) showed that sizes of catches from these collectors at each site provide a measure or index of the relative strength of settlement along the coast. Phillips (1986) used Seven Mile Beach as the "standard" site for the collection of puerulus data for catch prediction. Pueruli are collected at lunar monthly intervals. On occasion, therefore, two collections may be made in a calendar month: we have simply averaged the numbers of pueruli to give the settlement index for those months.

Pueruli indices used in this paper are from collectors deployed along the coast between September 1984 and December 1989. The nine sites were South Passage (Shark Bay), Horrocks Beach, Rat Island (Abrolhos), Seven Mile Beach, Jurien Bay, Cervantes, Alkimos, Warnbro Sound and Cape Mentelle (Kilcarnup) (Fig. 1). Logarithmic transformations were taken of the pueruli data.

Table 1

Correlation matrix of the logarithms of the monthly settlement indices at the nine sites between August 1984 and December 1989. SP = South Passage (Shark Bay); Hor = Horrocks Beach; Rat = Rat Island; SMB = Seven Mile Beach; Jur = Jurien Bay; Cer = Cervantes; Alk = Alkimos; WS = Warnbro Sound; CM = Cape Mentelle.

SP	1.000							
Hor	0.693	1.000						
Rat	0.620	0.784	1.000					
SMB	0.852	0.804	0.697	1.000				
Jur	0.816	0.739	0.707	0.861	1.000			
Cer	0.733	0.630	0.646	0.777	0.893	1.000		
Alk	0.571	0.614	0.555	0.756	0.740	0.710	1.000	
WS	0.595	0.506	0.403	0.668	0.661	0.724	0.825	1.000
CM	0.262	0.262	0.256	0.358	0.429	0.487	0.506	0.601
	SP	Hor	Rat	SMB	Jur	Cer	Alk	WS

A longer series of settlement indices covering 20 years at Seven Mile Beach and Jurien Bay (Phillips 1986) has also been used to check the validity of the conclusions from the five year series.

Oceanography

A number of environmental variables have been analysed to examine correlations with pueruli settlement.

Monthly mean values of the Southern Oscillation Index (SOI), computed from the Darwin and Tahiti mean sealevel pressures (Troup 1965), were supplied by the Australian Bureau of Meteorology. Monthly mean sealevels for Fremantle were obtained from the Flinders University Tidal Institute in Adelaide. Because of the difficulty of obtaining reliable wind measurements along the coast due to "contamination" by coastal land/sea effects, we obtained from the Bureau of Meteorology daily winds in 2.5 degree squares off Geraldton. These have been vector-averaged for the monthly means.

Sea temperature and salinity have been measured at intervals of two to three weeks at a monitoring station in 55 m water depth near Rottnest Island since 1970 (with a few measurements made in earlier years). Samples are taken at 10 m depth intervals between the water surface and the seabed; monthly depth-averaged values have been used in this paper.

Results

Correlations between the monthly (and total) puerulus settlement at the nine sites as well as cross correlations between the monthly puerulus settlement at the nine sites, SOI, sealevel, wind, water temperature and salinity have been undertaken.

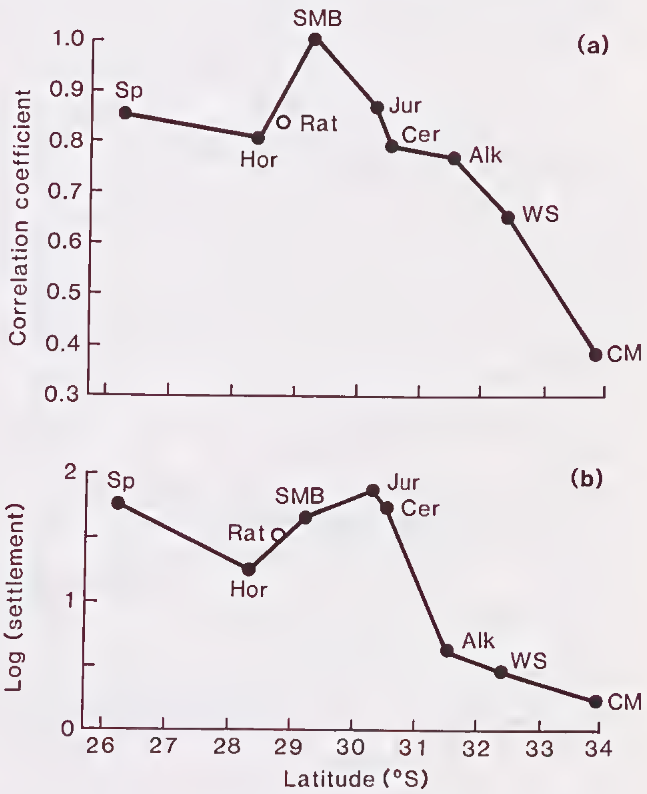

Figure 2 (a) Correlation of the monthly pueruli of *Panulirus cygnus* settlement from 1984-1989 at each of the 9 sites with that of the standard Seven Mile Beach site, after removal of the seasonal pattern. Rat Island has not been joined to the other sites by a line as that site is at the edge of the continental shelf, whereas all the others are on the coast. (b) Average pueruli settlement at each site over the full 64 month period.

Pueruli

The highest correlations of the monthly settlement (Table 1) were between Seven Mile Beach, Shark Bay, Horrocks Beach and Jurien Bay; Cervantes and Jurien Bay; and Warnbro Sound and Alkimos: whereas the correlations between Shark Bay, Horrocks Beach and Rat Island, and Cape Mentelle were low. The close correlation of the settlement at Rat Island, Jurien Bay and Seven Mile Beach was reported by Morgan *et al.* (1982). The correlation of the 20-year data set from Seven Mile Beach and Jurien Bay sites was high (0.804).

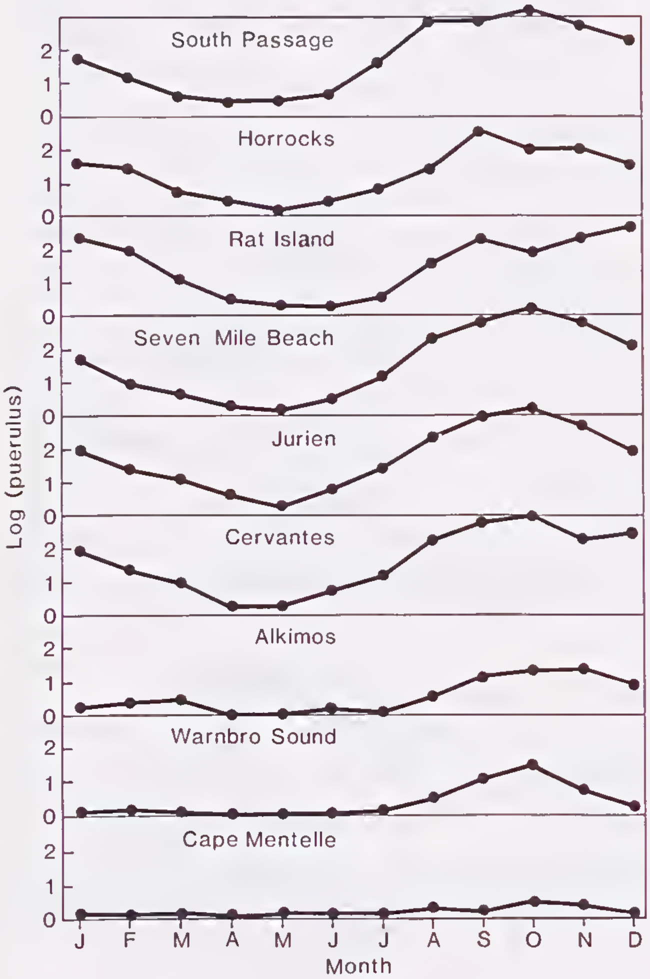

Figure 3 Monthly mean pueruli settlement (averaged over the 5 years) of *Panulir-us cygnus* at each site.

Correlation of the monthly settlement over the 5-year period with the "standard" Seven Mile Beach site (Fig. 2a) shows that the correlation decreases with distance from that location: the correlations are significant at the 99% level at all sites. The average settlement levels at the nine sites over the 5-year period (Fig. 2b) show a similar picture; with the highest levels of settlement occurring at Shark Bay, Jurien Bay and Cervantes, and that all these were higher than Seven Mile Beach while from the Alkimos southwards the settlement is generally low.

The mean seasonal pattern of puerulus settlement along the coast over the 5-year period 1984 to 1989 is shown in Fig. 3. Peak settlement tends to occur at all sites between August and December. Cross correlation (ccf) of the settlement at Seven Mile Beach with the other eight sites indicates that there is a tendency for settlement one month earlier at Cape Mentelle than Seven Mile Beach (ccf = 0.37), and one month later at Rat Island (ccf = 0.84). In some years, settlement began earlier in the season, or extended well into the following summer.

Pueruli anomalies

For all the datasets used in the further cross correlation analyses, the annual cycle has been removed, and the statistical analyses are therefore using the anomalies from the monthly means to check for association of one series with lags of another. The test statistics for cross correlations are only valid if each of the series has a zero autocorrelation function. Six of the nine puerulus series have significant autocorrelation functions as do three of the five environmental series. Therefore there are few valid tests. Diggle (1990) suggests the approximate formula $2/\sqrt{n}$ (= 0.25 in our case), where n is the total number of months, to assess the significance of the cross correlation function and the significance levels indicated are by this method. Due to the number of variables and the number of different lags being examined there may be some "significant" correlations which may be spurious.

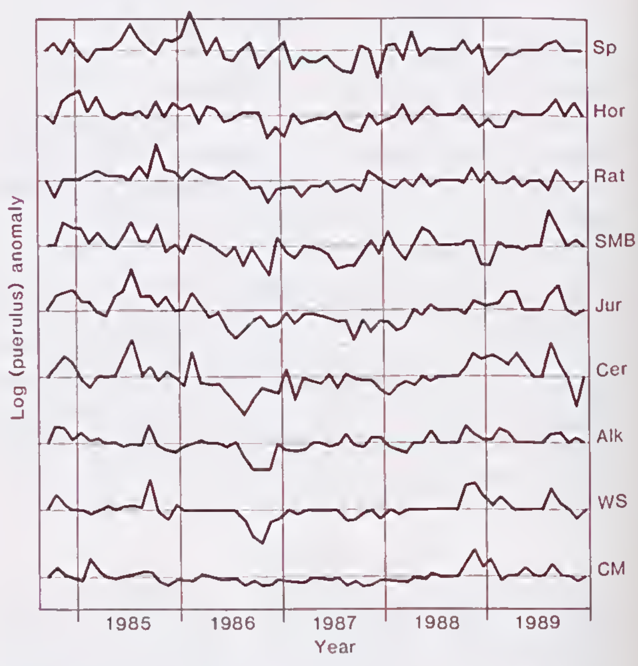

Figure 4 Anomalies in monthly pueruli settlement of *Panulirus cygnus* at the 9 collector sites between August 1984 and December 1989. The vertical axis is the logarithm of the settlement.

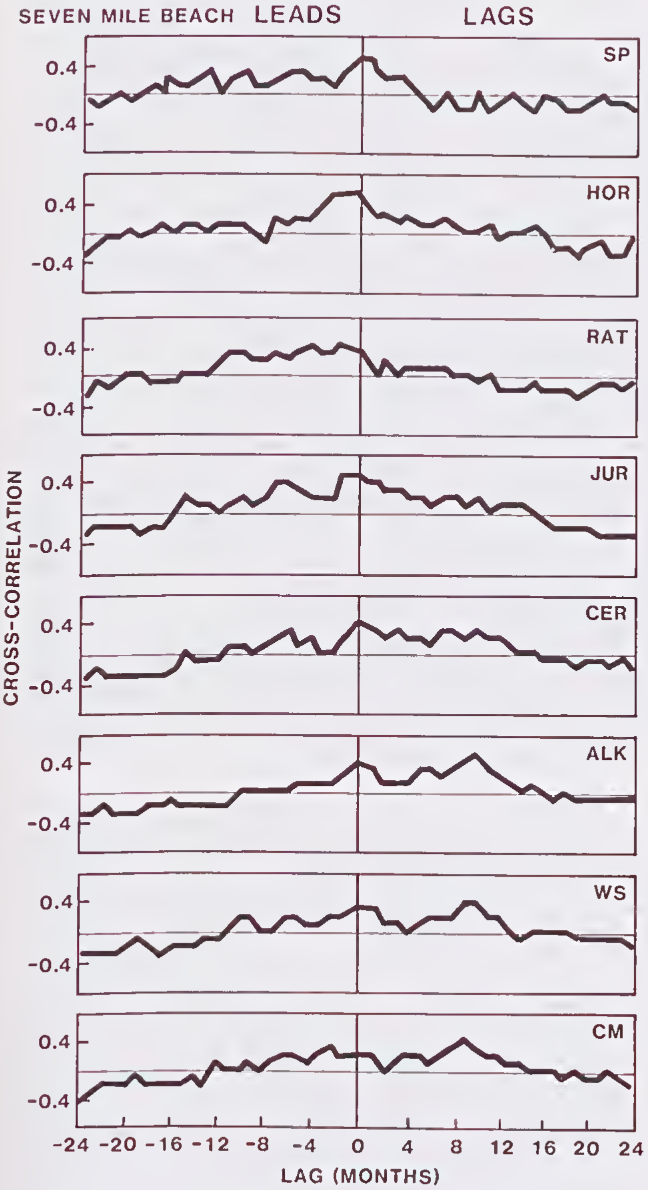

Figure 5 Cross correlations of pueruli of *Panulirus cygnus* at the 8 sites along the coast of Western Australia with the standard Seven Mile Beach site.

The anomalies in monthly settlement at the nine sites over the five year period 1984 to 1989 show both the alongshore and temporal variability in settlement (Fig. 4). The cross correlations of the anomalies in monthly settlement between Seven Mile Beach and the other eight locations (Fig. 5) indicate that there are different lag times in settlement with zero or short lags of two or four months in the northern sites from Shark Bay to Cervantes; versus longer lags of nine to ten months at the southern sites, Cape Mentelle, Warnbro Sound, Alkimos. The anomalies at Cape Mentelle, Warnbro Sound, Alkimos precede the Seven Mile Beach anomalies by 9-10 months. For example, the troughs in settlement that occurred late 1986 at Warnbro Sound, Alkimos and Cervantes do not occur till late 1987 in Seven Mile Beach, Horrocks Beach and Shark Bay (Fig. 4); and the peaks in Cape Mentelle, Warnbro Sound and Alkimos that occurred in late 1988 did not occur till late 1989 in Jurien Bay, Seven Mile Beach and Horrocks Beach. However, one must bear in mind that neighbouring locations are correlated and so a peak in one series is likely to be accompanied by peaks in the neighbour.

Pueruli and environmental variables

The maximum cross correlations and lags between the pueruli monthly series for 1984-1989 and the environmental series are shown in Table 2. The cross correlations of pueruli with wind (both north-south and east-west components) are low. The cross correlations of pueruli and SOI, Fremantle sealevel, Rottnest water temperature and salinity are all significant. The highest cross correlation was Cervantes pueruli one month after water temperature. Other high cross correlations are Jurien Bay pueruli three months after SOI or sealevel, one month after water temperature and zero lag with salinity.

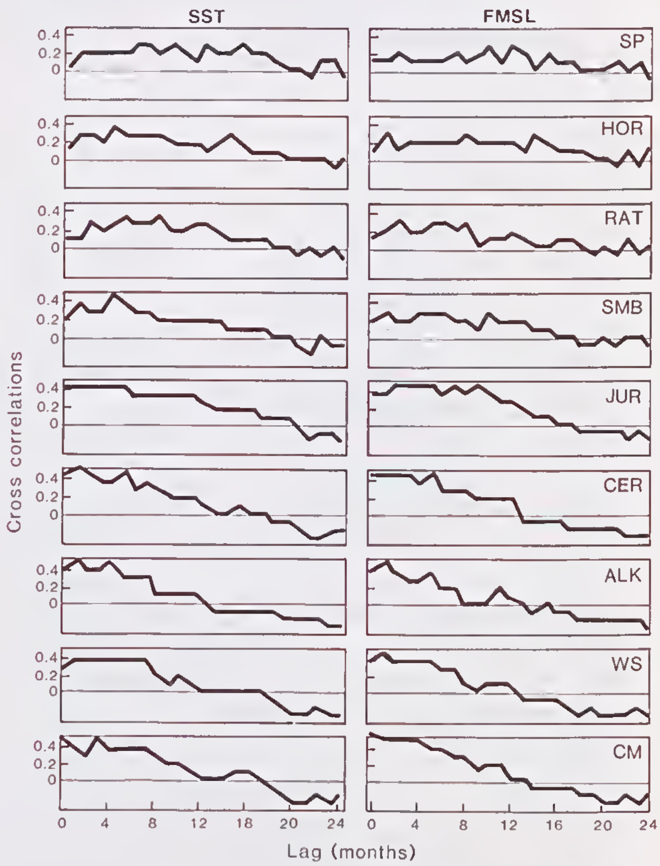

Figure 6 Cross correlations of pueruli settlement of *Panulirus cygnus* with Fremantle sealevel (FMSL) and water temperature (SST).

The cross correlation functions of pueruli for 1984-1989 with sealevel and water temperature are shown in Fig. 6. There was a broad trend of smaller lags (1-3

Table 2
The maximum cross correlations of pueruli with the environmental series (seasonal effects removed) showing maximum lags.

	SOI		Sealevel		SST		Salinity		East wind		North wind	
Site	max cross corr	lag (mths)	max cross corr	lag (mths)	max cross corr	lag (mths)	max cross corr	lag (mths)	max cross corr	lag (mths)	max cross corr	lag (mths)
SP	.23	3	.32	10	.33	9	-.33	15	-.26	0	.24	0
Hor	.24	8	.32	8	.38	4	-.37	1	-.29	6	-.23	8
Rat	.35	0	.30	8	.43	9	-.24	5	-.21	1	-.27	8
SMB	.27	3	.29	10	.53	4	-.37	6	-.36	3	-.29	8
Jur	.51	3	.51	3	.51	1	-.57	0	.17	6	-.28	4
Cer	.49	3	.50	3	.62	1	-.48	0	.27	11	-.42	1
Alk	.30	1	.50	1	.50	4	-.38	0	.25	5	-.35	3
W S	.43	1	.47	1	.45	1 or 5	-.31	0	.21	5	-.37	3
CM	.50	3	.56	0	.46	3	-.52	0	.19	4	-.34	4

months) for the southern sites (Cape Mentelle, Warnbro Sound, Alkimos, Cervantes, Jurien Bay), with sealevel and water temperature to larger lags (4-10 months) for the northern sites (Seven Mile Beach, Rat Island, Horrocks Beach, Shark Bay). This trend is also evident with salinity.

A similar cross correlation analysis of the longer time settlement data from Seven Mile Beach and Jurien Bay against sealevel showed that the maximum cross correlation (0.27) occurred when settlement at Jurien Bay lagged Fremantle sealevel by four months and when Seven Mile Beach lagged Fremantle sealevel by four months (0.26).

Satellite imagery

We also attempted to relate mesoscale (order 100 km) features of the Leeuwin Current as revealed by satellite images to fluctuations in puerulus settlement along the coast. Pearce & Phillips (1988) suggested, for example, that a strong meander off Geraldton in October 1984 may have contributed to the record settlement at Seven Mile Beach in that month.

While there is little doubt that meanders offshore of the Leeuwin Current can rapidly bring phyllosoma larvae towards the shelf (Pearce & Phillips 1992), current measurements along the shelf break have shown that the alongshore flow is very strong (Cresswell *et al.* 1989). It now seems more likely, therefore, that the pueruli will be carried both south and north by the reversing current system on the shelf and so distributed over a larger area of coastline.

Along the inshore boundary of the Current, settlement may be aided or hindered by variations in the currents or water temperature near the coast. For example, zero settlement at Cape Mentelle in 1986 and 1987 (both ENSO years when low coastal sealevels indicated a weak Leeuwin Current) was possibly associated with the Leeuwin Current being along the outer shelf and a cool inshore counter-current in that area (Fig. 7a). In 1988, on the other hand, there was appreciable settlement at Cape Mentelle, and satellite imagery for November 1988 showed warm Leeuwin Current water flooding onto the shelf (Fig. 7b).

Discussion

Spatial and temporal settlement of puerulus

It is clear that settlement along the coast of Western Australia follows a similar seasonal pattern at all sites and that in years when settlement occurs there is a close correlation between adjacent sites. However, the

Figure 7 Satellite images of South-Western Australia from the NOAA Advanced Very High Resolution Radiometer (AVHRR): (upper) orbit N9/15219 on 26 November 1987, and (lower) orbit N11/646 on 9 November 1988. The Leeuwin Current is evident as the warm (pale) water along the shelf. The area shown is from Fremantle (in the north) to south of Cape Leeuwin; Cape Mentelle is midway between the two prominent capes (Cape Naturaliste and Cape Leeuwin). Images courtesy of the Western Australian Satellite Technology and Applications Consortium (WASTAC).

southern sites receive lower levels of settlement than in the north, and in some years have zero settlement.

Both 1986 and 1987, the two years in which no settlement was recorded at the southern sites, were ENSO years when the Leeuwin Current was weaker. Settlement to the southern area may only occur (or be higher) when the Leeuwin Current is strong and running close inshore. Catches in the southern area of the fishery fluctuate much more than in the central and northern areas of the fishery, supporting this hypothesis.

Correlation between environmental events and levels of pueruli settlement

Only preliminary conclusions can be drawn from the results in view of the short time span of the data. Phillips (1986) recorded fluctuations in the annual index of puerulus settlement at Seven Mile Beach ranging from 15.9 to 182.8 over a 14-year period. Between 1984 and 1989 the values ranged from 60.3 to 128.4, hence it is difficult to assess the exact reliability of the cross correlations recorded. However, the strong cross correlations of SOI, sealevel, sea surface temperature and salinity with settlement at all sites indicate that similar forces are affecting settlement along the whole coast. This is in line with the conclusions of Pearce & Phillips (1988) who suggested that the oceanic processes influencing settlement along the Western Australian coastline operate at length scales of the order of hundreds of kilometres and time scales of many months to a year.

Of the environmental factors examined in this study, sealevel, sea surface temperature and salinity may all reflect interrelated expressions of monthly to annual variations in the strength or temperature of the Leeuwin Current.

Some of the correlations are curious. It is, for example, difficult to imagine the basis for the between-season time lags of puerulus settlement where the northern sites, such as Seven Mile Beach, follow settlement at the southern sites nine to ten months later. However, the long term (20-year) data from Seven Mile Beach and Jurien Bay show the same picture. This may point to previously unrecognised linkages in oceanic events.

Although Pearce & Phillips (1988) demonstrated that there is a clear link between the Leeuwin Current and larval recruitment, the mechanisms which act on the larval or puerulus stage to bring this about are as yet unknown. This is partly because of a lack of information about the site of transformation to, and the behaviour of, the puerulus stage, as well as variability of the oceanic environment. Further studies of both these aspects are necessary.

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The influence of the Leeuwin Current on coastal fisheries of Western Australia

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Abstract

The fisheries of the three major southern hemisphere eastern boundary currents are briefly reviewed. In all three systems, physical environmental variables influence fish catches in a major way. Both the Benguela and Humboldt Currents create highly productive and dynamic upwelling ecosystems that are characterised by a succession of dominant finfish species, which can individually support substantial commercial fisheries. By contrast, the Leeuwin Current waters off the west coast of Australia are characterised by low biological productivity. Although a group of finfish species, almost identical to those of the Benguela and Humboldt Current ecosystems is represented in the Leeuwin Current ecosystem, the collective Western Australian catches of these species are insignificant by world standards. Indeed the major commercial species of this region are demersal invertebrates, some of which (*eg* rock lobster) support fisheries of international significance. Thus the Leeuwin Current does exert a major influence on the overall ecology of this unique region, and affects the production of both economically important finfish and invertebrate species.

Introduction

Historically four major eastern boundary current systems were recognised in the world oceans (Wooster & Reid 1963). They comprise very large spatial systems which exhibit unique bathymetry, circulation, biological productivity and trophodynamic relationships of populations. Two of these, the California and Canary Currents, are located in the northern hemisphere, while the other two, the Humboldt and Benguela, are located in the southern hemisphere (Parrish *et al.* 1983, Weaver 1990).

Both the Humboldt and Benguela eastern boundary currents are part of oceanic-scale wind-driven anticyclonic gyres in the southern hemisphere. Because the equatorward flow of water is in the same direction as the prevailing wind, upwelling is associated with these coastal currents (Cushing 1971, Shannon 1985, Bohle-Carbonell 1989). In recent years, however, a fifth and uniquely different eastern boundary current system has been recognised (Golding & Symonds 1978, Cresswell & Golding 1980, Pearce & Phillips 1988, Pearce & Prata 1989). In contrast to the other four eastern boundary current systems, the Leeuwin Current is driven poleward by a deep alongshore density gradient, whose existence is partly dependent on the flow of warm western equatorial Pacific water through the Indonesian Archipelago (Weaver 1990). The lack of upwelling associated with this current is because of the eastward flow of Indian Ocean water despite the prevailing southerly winds (Godfrey & Ridgway 1985).

The life history characteristics, such as spawning, migration, recruitment and feeding patterns, and ultimately the overall production of many ecologically important finfish species have evolved under the influence of such current systems.

For example, the upwelling of cool nutrient-rich water, which is a most important characteristic of the Humboldt/Benguela systems leads to high rates of primary production *ie* high biomass of phytoplankton and zooplankton (Cushing 1971, Armstrong *et al.* 1987, Chavez *et al.* 1989). This accounts for the substantial populations of pelagic planktivorous fishes found in both of these upwelling systems (Crawford *et al.* 1983, Parrish *et al.* 1983, Crawford *et al.* 1987, Crawford 1987). Indeed the commercial catches of pelagic species from these regions are very significant in the context of world fish production (FAO 1988).

By contrast, the Leeuwin Current consists of warm low nutrient water flowing into continental shelf waters,

Table 1

The prominent families of finfish which comprised the commercial catch from southern hemisphere eastern boundary currents systems during the 1980's.

Finfish Families	Southern Hemisphere Eastern Boundary Current Systems Humboldt	Benguela	Leeuwin
Clupeidae (true herrings)	Sardine	Pilchard Round herring Sardinella	Pilchard Round herring (maray) Sardinella
Engraulididae (anchovy)	Anchoveta	Anchovy	Anchovy
Carangidae (trevally)	Horse mackerel	Horse mackerel	= Jack mackerel (or scad)
Scombridae (mackerel)	Mackerel Bonito	Mackerel Bonito	Mackerel Bonito
Merluccidae (hake)	Hake	Hake	?(offshore)
Gemplylidae (snoek)		Snoek	Barracouta (or snoek)
OVERALL ANNUAL CATCH (Million tonnes)	<1-13*	<1-4*	<0.001+

Source * FAO, 1988, Crawford *et al*, 1987
+ Anon. 1990

which, by Humboldt/Benguela standards, are already low in nutrients (Rochford 1980, 1988, Pearce *et al.* 1985). Although similar pelagic planktivorous fish species are represented in the Leeuwin Current system, the commercial catches of these species are far smaller than those of similar species taken from the Benguela and Humboldt upwelling regions (Table 1). Indeed, demersal species (particularly rock lobster and prawns), that are dependent on benthic production dominate commercial catches taken from the Leeuwin current (Anon. 1990).

Effect of the Humboldt and Benguela Currents on Associated Fisheries

Environmental change, rather than factors such as recruitment overfishing, predation or pollution, has been identified as the major variable controlling large scale changes in fish abundance in all eastern boundary currents (Sherman 1987).

Understanding the complex processes through which, in an overriding sense, climate (Cushing 1982, Sharp 1987) and more specifically the physical environmental properties of the current systems can ultimately affect commercial fish catches is of major importance to the managers of such fisheries.

Principal abiotic properties of the current environment that can lead directly to changes in fish abundance (and therefore catches) include: current strength and direction, current motion (or turbulence), water temperature, water salinity, and dissolved oxygen. For example, temperature, turbulence and transport patterns influence the location of spawning grounds and the breeding period of anchovies and pilchards in those eastern boundary currents characterised by upwelling (Parrish *et al.* 1983).

Certainly, instances of strong recruitment for neritic stocks in the southern Benguela system have been linked to environmental anomalies (Crawford *et al.* 1983). Specifically, sea surface temperature and anchovy recruitment have been positively correlated (Boyd 1979). Sea temperature has also been shown to influence directly the survival of pilchard and anchovy eggs (King 1977).

Furthermore, a shift of the predominant species from anchoveta to sardine between 1970 and 1983 resulted in a dramatic increase in the yield of sardine off Chile and Peru (Cushing 1982). This has been partially attributed to El Niño producing higher sea surface temperatures which in turn reduced the anchoveta habitat size (Muck 1989a), and thereby made them more vulnerable to fishing pressure (Cushing 1982, Csirke 1989).

The above abiotic factors can also indirectly affect abundance of important commercial fish species by influencing their food supply, competitors and predators (Wooster & Bailey 1989).

For example, high sea surface temperatures associated with El Niño events can indirectly reduce anchoveta abundance by increasing the density-dependent mortality on eggs and larvae, increasing metabolic cost and reducing food availability (Muck 1989a). Moreover, the intrusion of warm oxygen-rich waters from the north into the Humboldt upwelling system during El Niño events, led to hake extending further south, and thus invading the main anchoveta area. This allowed increased anchoveta predation of hake eggs (Muck 1989b).

Effect of the Leeuwin Current on Fisheries Productivity

The continental shelf waters off Western Australia are relatively low in nutrients (Pearce *et al.* 1985) and relatively clear. As a result of the Leeuwin Current, the overall temperature range in the region of its influence is also relatively small. Temperatures are therefore appreciably warmer than at comparable latitudes in other eastern boundary current regions (Pearce 1991).

Because of the shape of the Western Australian coastline, and in particular variation in the width of the continental shelf, the impact of the Leeuwin Current appears to be greater on some sections of the shelf than others. Satellite imagery has suggested that the current approaches the coastline between North-West Cape and Shark Bay, in the Geographe Bay/Cape Naturaliste/Cape Leeuwin region, and along the south coast from Pt. D'Entrecasteaux to about Albany (Pearce 1985). In addition, islands near the edge of the shelf, such as the Abrolhos Islands and Rottnest Island, are particularly affected by the warm current waters (Hatcher 1991, Hutchins 1991).

Because upwelling is not a feature of the current system, nutrient levels in the coastal waters are largely dependent on terrestrial inputs. Run-off from the largely arid hinterland is particularly low, with the limited river outflow mostly from the south-western region of the State being confined almost entirely to winter/spring (Lenanton & Hodgkin 1985). The relatively clear coastal waters landward of the Leeuwin Current, which include the large marine embayments of Shark Bay and Geographe Bay, are typified by extensive seagrass meadows and macroalgae dominated coastal reef systems (Kirkman 1985, Walker 1991). Coastal finfish resources of the state are generally confined within these water masses landward of the main current and are largely dependent on the relatively productive estuarine and protected coastal marine ecosystems (Lenanton 1982, Robertson & Lenanton 1984, Lenanton & Potter 1987).

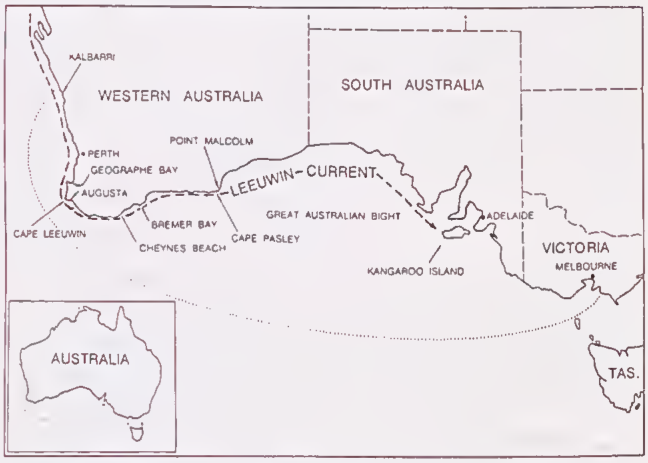

Figure 1 The limits of distribution of the Western Australian salmon. Hatching indicates the region of most intensive spawning. In addition to these major fisheries, there are also tropical species appearing in the commercial and recreational catch off the west coast which are dependent on the seasonal flow of the Leeuwin Current (Maxwell & Cresswell 1981, Hutchins 1991).

The major invertebrate resources of Western Australia, the western rock lobster *Panulirus cygnus* (Phillips & Brown 1989), and penaeid prawns *Penaeus esculentus* and *Penaeus latisulcatus* (Penn 1981), are similarly dependent on the extensive inshore and relatively productive macrophyte zones.

Fisheries Affected by the Leeuwin Current

Almost all of the major economically important fish stocks in waters off the western and southern coasts of Western Australia are influenced to some extent by the Leeuwin Current. As will be shown below, fisheries which are specifically affected by the current are (i) the Western Australian salmon and herring fisheries off the south and lower west coasts; (ii) the pilchard purse seine fishery off the south coast; (iii) the western rock lobster fishery off the west coast; (iv) the saucer scallop fisheries in Shark Bay and other areas off the west and

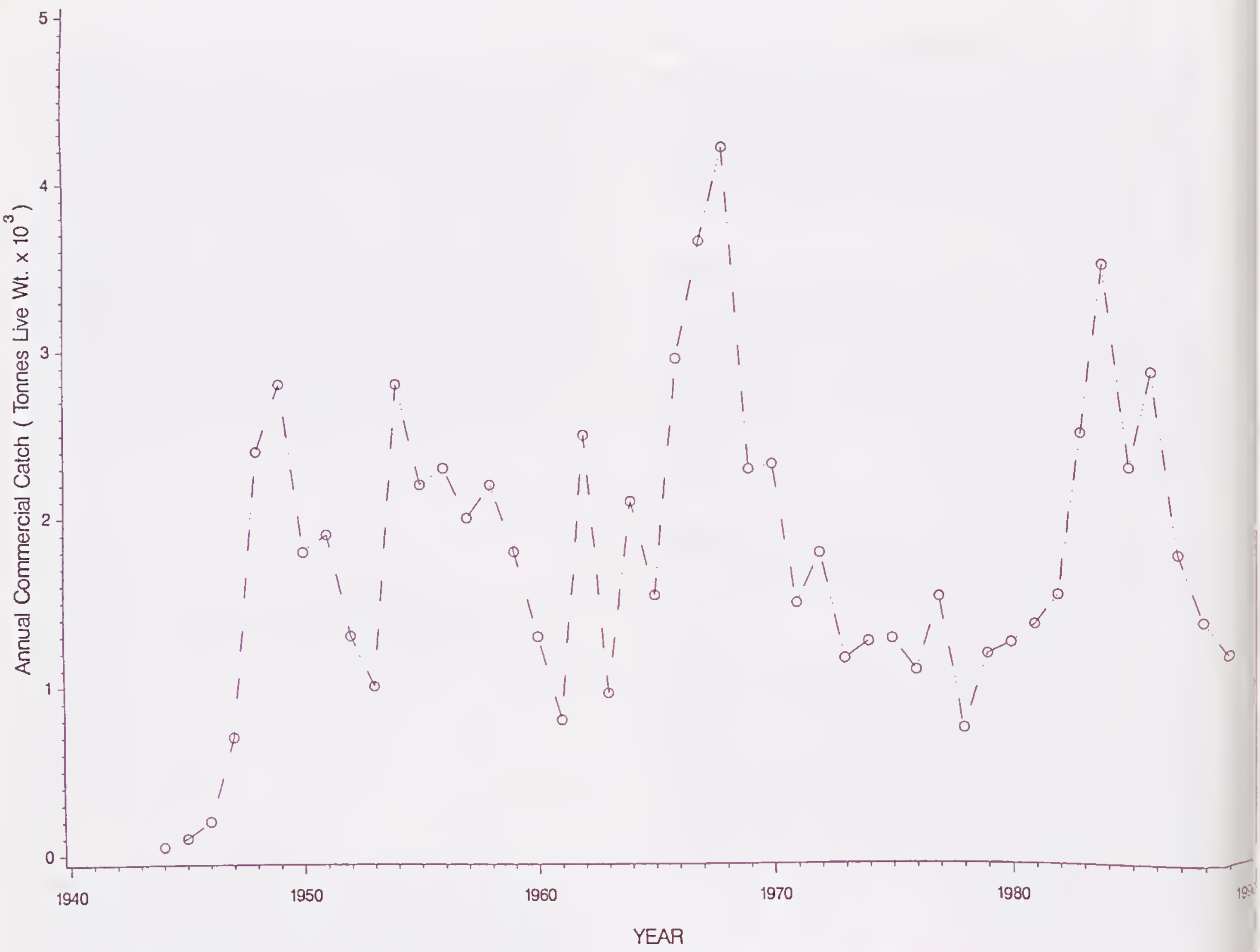

Figure 2 The annual Western Australian commercial catch of Western Australian salmon between 1944 and 1989.

south coasts; and (v) the penaeid prawn fishery in Shark Bay.

They include scaly mackerel (*Sardinella lemura*), dusky (bronze) whaler shark (*Carcharhinus obscurus*), spanish mackerel (*Scomberomorus* spp.) and baldchin groper (*Choerodon rubescens*) in marine waters; and bar-tailed flathead (*Platycephalus endrachtensis*) and giant herring (*Elops machnata*) in the Swan river system.

A large component of the finfish catch from the Abrolhos Islands is also made up of tropical species such as narrow-barred spanish mackerel (*Scomberomorus commerson*), cod (*Epinephelus spp.*), coral trout (*Plectropomus* spp.) and baldchin groper.

Western Australian salmon fishery

Western Australian salmon (*Arripis truttaceus*) is a large pelagic inshore schooling species (Malcolm 1960). It is distributed from Kalbarri on the mid-west coast of Western Australia to about Victoria and western Tasmania on the south coast of Australia (Fig. 1) (Stanley 1980a, Hutchins & Swainston 1986) where it supports substantial commercial net and recreational angling fisheries (Stanley 1980a, Walker 1982, Cappo 1987).

The major Western Australian fishery for salmon is located off the beaches between Geographe Bay and just east of Bremer Bay (Stanley 1980a, Walker 1982). All fish located east of the western Great Australian Bight are immature (Malcolm 1960, Stanley 1980a, 1980b), while all the mature fish are located in Western Australian waters.

Spawning commences during March, and reaches a peak during early April (Malcolm 1960, Nicholls 1973). It is postulated that large numbers of fertilised eggs and larvae are transported east by the Leeuwin Current to inshore protected nursery grounds located between the western Bight and Victoria (Cresswell 1986, Malcolm 1960, Robertson 1982).

Juveniles first appear in the Western Australian nursery grounds in April (Lenanton 1977, 1982), and in

South Australia, nursery grounds in June (Jones *et al.* unpublished). Although juveniles are first fished commercially as 1 year old fish in South Australia (Stanley 1979, Cappo 1987), there is very little commercial exploitation of juveniles in Western Australia (Walker 1982). Fish tend to mature according to size rather than age, and grow much faster in Western Australia than in eastern Australia (Nicholls 1973, Stanley 1979, 1980b).

At about the end of January/early February, mature and maturing fish migrate from waters adjacent to their nursery grounds west to spawn off the lower west and south coasts of Western Australia (Malcolm 1960, Stanley 1980a). These fish form the basis of the Western Australian commercial and recreational fishery (Walker 1982, Cappo 1987).

At the beginning of each season, the Western Australian catch comprises mainly larger resident fish (Malcolm 1960, Stanley 1980a). By about mid March, smaller new recruits dominate the catch (Stanley 1980b, Cappo 1987).

Preliminary modelling of the Western Australian salmon fisheries has revealed that stock abundance appears to be dependent mostly on the magnitude of annual recruitment. Major peaks in annual Western Australian catch, in particular those in the late 1960's and early 1980's (Fig.2) are thought to be related to periods of strong recruitment from Western Australian nursery areas (C. Walters, R.C.J. Lenanton and M. Cappo, unpublished). Furthermore environmental change influenced by the Leeuwin Current, rather than fishing, appears likely to be one of the main factors affecting recruitment.

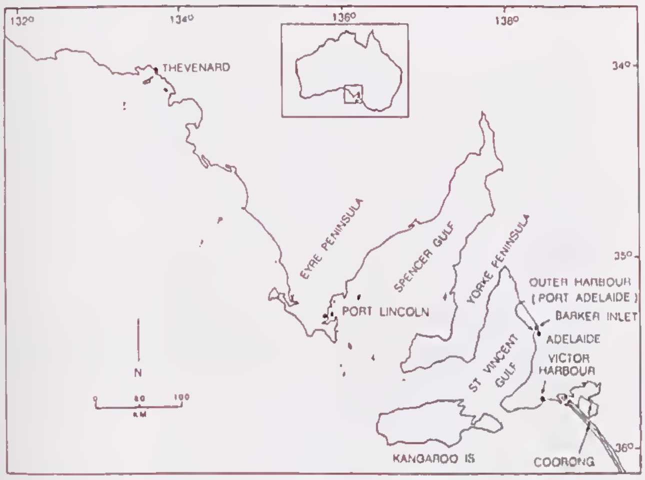

Figure 3 Central and western coastline of South Australia showing sites where sealevel is routinely monitored, together with sites where juvenile salmon abundance is measured.

Preliminary evidence from South Australia suggests that the Leeuwin Current assists the recruitment of salmon to South Australian nursery areas. First a significant positive correlation has been demonstrated between the Southern Oscillation Index (SOI) and mean annual sealevel at Thevenard ($r^2=0.42$, $0.025<P>0.05$), Port Lincoln ($r^2=0.35$, $0.0025<P>0.005$), Port Adelaide (Outer Harbour) ($r^2=0.46$, $0.005<P>0.025$) and Victor Harbor ($r^2=0.50$, $P=0.01$) (Fig. 3). In years of low SOI (and weak Leeuwin Current) (*eg* 1982), relatively low sealevels occurred during June to September when 0+ year old salmon are being distributed across the Great Australian Bight and entering the nursery areas of the west coast bays, South Australian Gulfs and the Coorong waters (Fig.4). In years of high SOI (and strong Leeuwin Current) (*eg* 1981), the sealevel during these months was relatively high.

An annual recruitment index (natural log numbers (ln n)) of 0+ year old salmon is available between 1980 and 1990 from the waters of Barker Inlet, adjacent to the Outer Harbour in South Australia (Fig.3) (G.K. Jones, G. Wright & K. Edyvane, unpublished). Further analysis revealed a significant positive correlation between sealevel in August (the usual month when salmon enter the South Australian nursery areas) at Outer Harbour, and the annual recruitment Index of salmon in Barker Inlet (Fig.5).

The commercial catch of salmon in waters of the Coorong comprises mainly 1+ year old fish (Cappo 1987). There is also a significant positive correlation between the commercial catches of 1+ year old salmon in the Coorong waters and the adjacent Victor Harbor August sealevel measured one year earlier (Fig.6).

Thus, there is strong circumstantial evidence for a direct, relatively short-term (up to 6 months) process of transportation of larvae from Western Australian spawning areas to South Australian nursery areas. Furthermore, there are indications that both current strength and timing of peak flow are likely to have an important influence on the strength of recruitment to South Australian nursery areas.

Attempts to relate mean sealevel at Albany at the time of spawning to the subsequent recruitment of maturing salmon into the Western Australian commercial fishery (*ie* between 4 to 6 years later) have to date been unsuccessful because of:

1) the complicated size-dependent recruitment process

2) variable annual rates of fishing and natural mortality during the relatively long period of four or more years leading up to recruitment into the fishery.

However, there are indications that commercial catches may be adversely affected in years of strong Leeuwin Current flow along the south coast of Western Australia. Preliminary analyses have revealed a negative correlation between the mean monthly sealevel at Albany over the period of the fishery (February - April) and the mean annual south coast log book catch per hour of beach observation in that same year (Fig.7). These data were treated as two separate

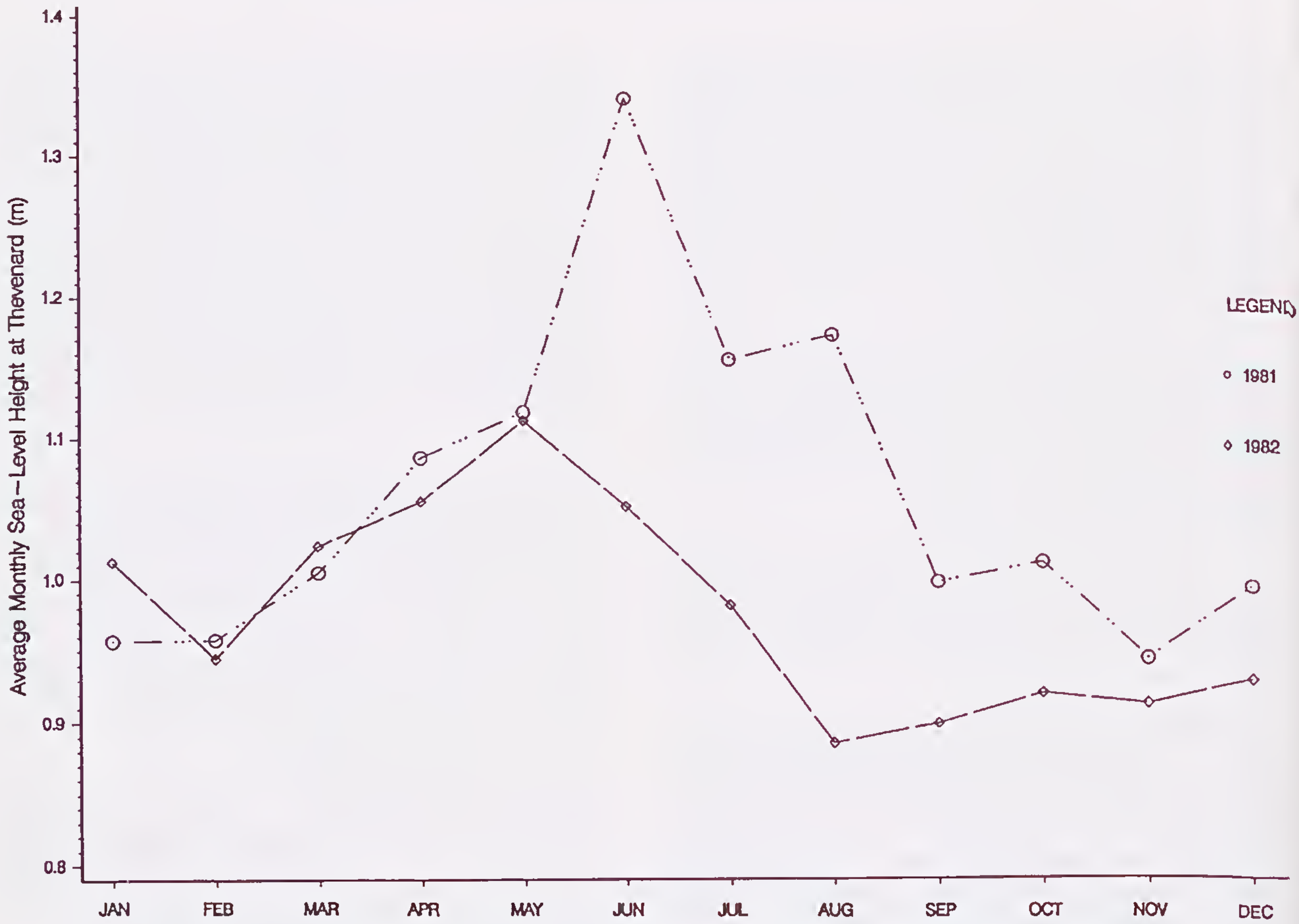

Figure 4 The average monthly sealevel at Thevenard, South Australia during years of weak (1982) and strong (1981) SOI.

groups: those from years of low catches (=abundance) and those from years of high catches.

The suggestion, supported by observations from commercial fishers, is that in years of strong Leeuwin Current flow, local storm events modify the pattern of the current flow, resulting in "patches" of warmer Leeuwin Current water adjacent to the shoreline. Thus, migrating salmon are forced offshore and deeper, in order to avoid these cells of warmer water, and at such times are not available for capture on beaches located along the affected shoreline. Thus during years of strong Leeuwin current flow the catchability of the stock is reduced.

Indeed, log book records kept by two demersal shark gill net fishers (Table 2) show clearly that salmon occurred within 3 m (the approximate depth of the nets) of the bottom in water depths of up to 57 m. Further, a by-catch of salmon has consistently been recorded in the monthly catch and effort returns of a number of demersal gill net fishers who operate in a variety of areas between Geographe Bay and Cheynes Beach (Fig.1).

Although the above data suggest that the Leeuwin Current is the major factor influencing larval transport and distribution, the precise details of the process are not known. Observations by fishers suggests that salmon spawn close to the coast. However the Leeuwin Current usually flows along the shelf break. Thus if the current is in fact the medium of larval transport, then either the fish must spawn in locations where the current is close to the coast (*eg* in the Cape Naturaliste region), or other factors such as local weather conditions must contribute to the transport of fertilised eggs offshore into Leeuwin current waters.

If the timing of peak current flow coincided with peak spawning, maximum numbers of larvae could be expected to be transported via the current. Then there is the question of what factors influence the relative size of recruitment to the different shoreline nursery areas located off the southern Australian coast. Do local weather conditions play an important role? Are the larvae transported in a frontal system associated with the current? How are potential competitors/predators affected by the current? Clearly the processes involved are only just beginning to be understood.

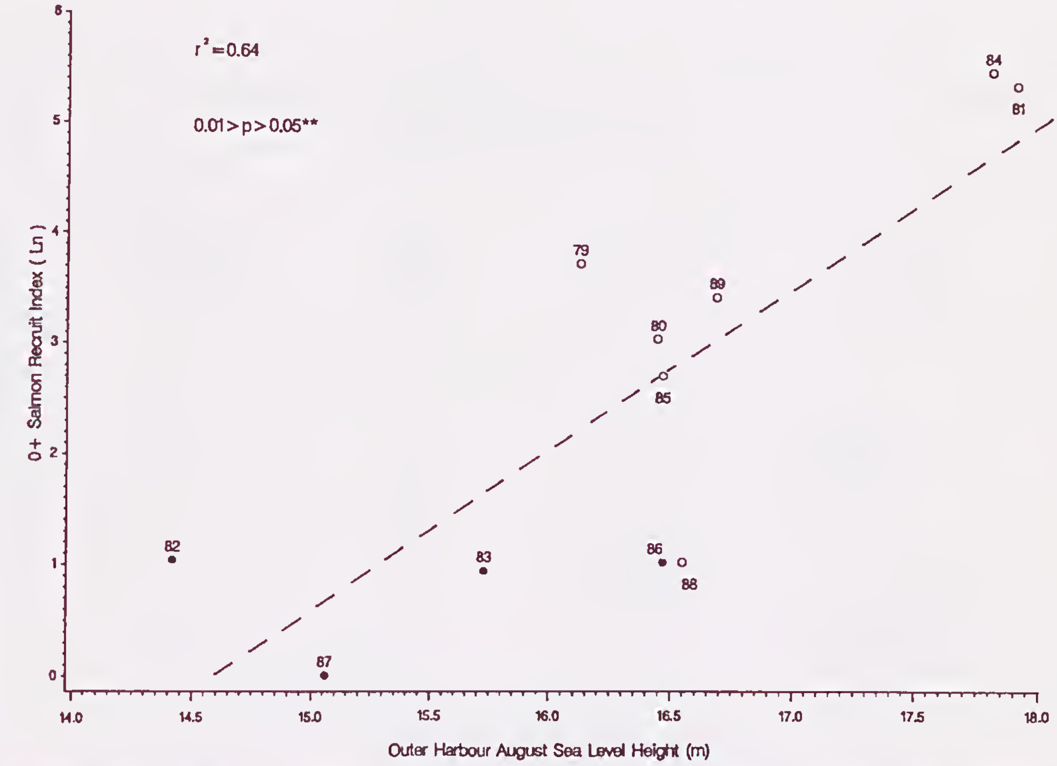

Figure 5 Relationship between the annual recruitment index (ln n) of salmon in Barker Inlet, and the sealevel in August at Outer Harbour over the period 1979-89 (83 = year of data; ● ENSO years ○ Non-ENSO years).

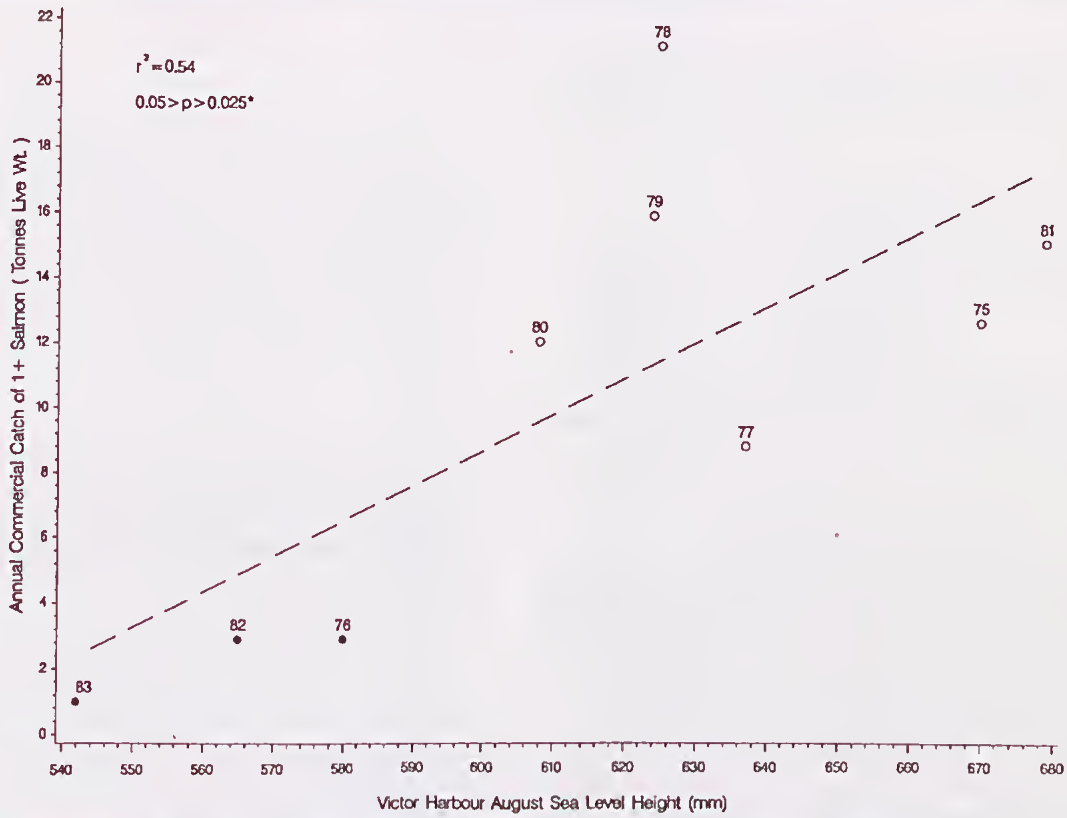

Figure 6 Relationship between the annual commercial catch of 0+ year old salmon caught in the Coorong between 1976/77 and 1984/85 and the Victor Harbor sealevel in August one year earlier (83 = year of data; ● ENSO years ○ Non-ENSO years).

Table 2

Western Australian salmon by-catch records extracted from log books kept by two demersal longline and demersal gill net limited entry fishers.

Date	Fishing area (see Fig. 1)	Location	Depth (m)	Surface water temp (°C)	WA salmon catch
1990					
290390	Augusta	34°43'S 115°18.4'E	50	20.1	500 kg
300390	Augusta	34°38.5'S 115°14.6'E	47	21.2	+
070490	Augusta	34°43'S 115°15.3'E	50	21.2	+
080490	Augusta	34°41.6'S 115°16.5'E	47	21.6	+
130490	Augusta	34°27'S 115°27.2'E	38	20.3	+
140490	Augusta	34°26.7'S 115° 27.7'E	38	20.5	+
1991					
210291	Cape Pasley/ Pt. Malcolm	33°49'S 124°0'E	57	20.8	7 fish
050391	Cape Pasley/ Pt. Malcolm	34°02'S 123°40'E	55	21.1	5 fish

+ WA Salmon were caught but precise quantities were not recorded

Australian herring fishery

The stock of Australian herring (*Arripis georgianus*) occupies an almost identical range to salmon, extending from Kalbarri to South Australia and into Victoria (Fig. 1). Like salmon, herring spawn predominantly on the lower west and western south coasts of Western Australia (Lenanton 1978), while the juveniles extend through the Great Australian Bight into South Australia and Victoria. A pre-spawning migration to Western Australia occurs for the first time during the second year of life. The source of recruitment ranges from South Australia and the G.A.Bight region to local marine embayments, particularly Geographe Bay, where juveniles occur abundantly, associated with seagrass and drift macrophytes in the waters inshore of the Leeuwin Current (Lenanton 1982).

Ongoing research (G.K. Jones, unpublished) is providing preliminary evidence for a direct link between the abundance of juveniles in South Australia and the size of the spawning stock in Western Australia. Thus it is highly likely that the strong Leeuwin Current flow at the time of spawning in autumn is a critical factor in the transport of larvae across the G.A.Bight to South Australian and Victorian nursery areas.

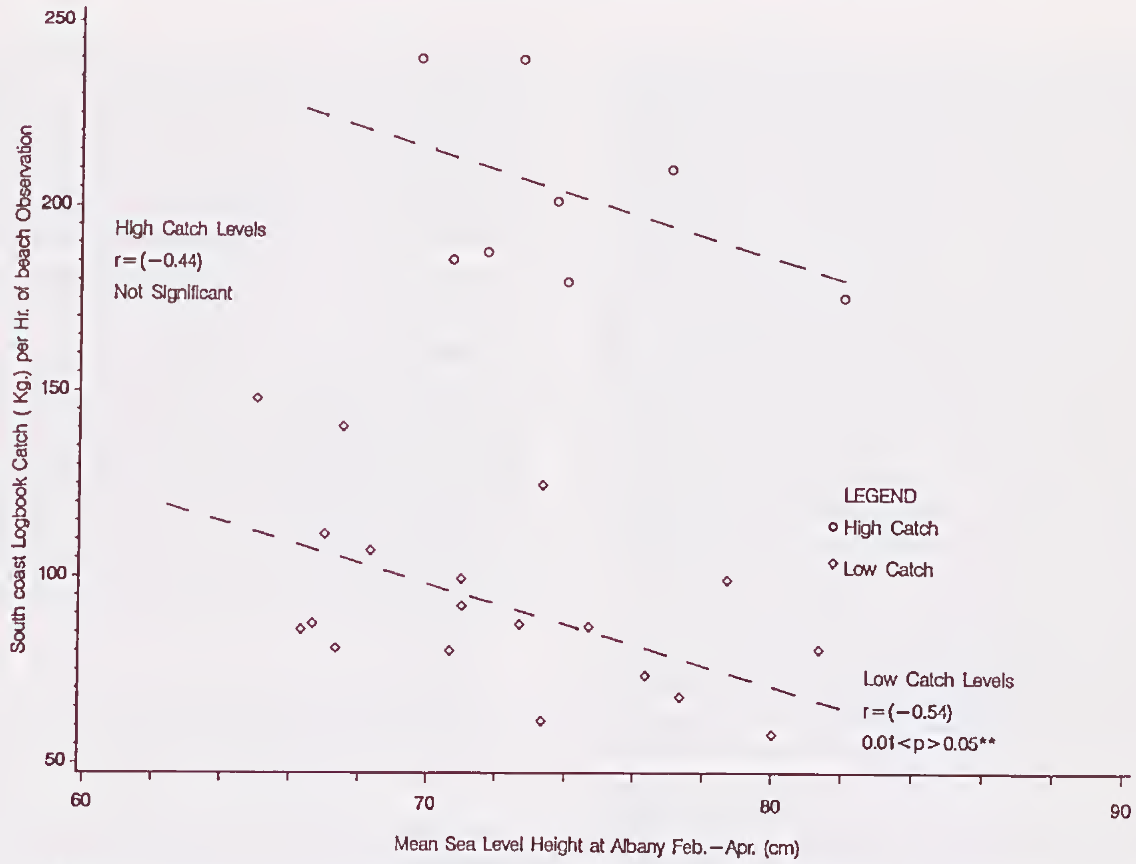

Figure 7 Relationship between the mean monthly Albany sealevel between February and April, and the mean annual south coast log book catch of salmon per hour of beach observation during years of low and high annual catch.

Pilchard purse seine fishery

The stock of pilchards (*Sardinops neopilchardus*) on the south coast, centred on King George Sound at Albany, provides Western Australia's largest single catch of finfish (Fletcher 1990). The fishery, which has developed over the past decade, reached a peak in catch of 8 300 tonnes in 1988, but has subsequently declined to less than 6 500 t annually (W.J. Fletcher, unpubl).

This species is either closely related to, or the same species as, the dominant *Sardinops* species in the Humboldt and Benguela Currents (Table 1, Parrish *et al.* 1989). However, catches in Western Australia to date indicate that maximum sustainable production is likely to be around 10 000 t which is orders of magnitude lower than catches of the same or similar planktivorous species in the other current systems (FAO 1988).

Survey data (W.J. Fletcher & R.J. Tregonning, unpublished) has shown that the species in Western Australia is found predominantly close inshore and therefore is taken only in bays, usually within the 50 m depth contour. Thus the Leeuwin Current significantly reduces the production of pilchards in this region compared to other boundary current systems. Furthermore, analyses of commercial catch rates, together with computer modeling (W.J. Fletcher, unpubl), suggest that yearly fluctuations in current strength are probably involved in the larger variations in the observed catch.

Western rock lobster fishery

The western rock lobster (*Panulirus cygnus*) stock supporting Australia's most valuable single species fishery is directly influenced by the Leeuwin Current and other environmental factors.

Phillips *et al.* (1991) and Pearce & Phillips (1992) deal in detail with the impact of the current on the recruitment of the puerulus stage of the life history. These studies have shown that the levels of puerulus settlement in the nursery grounds on the coast are highly correlated with sealevel changes which provide an index of the Leeuwin Current strength (Pearce & Phillips 1988), and with westerly storm conditions during the settlement period (Caputi & Brown 1989). Once settled, the juvenile lobsters remain for approximately 4 to 5 years on the coastal limestone reefs while feeding on the fauna and flora associated with seagrass beds (Joll & Phillips 1984). Thus the Leeuwin Current, which not only regulates recruitment to the stock but maintains the clear water environment essential to the development and survival of the extensive seagrass beds, is closely linked to the overall production of the fishery.

A second and possibly more critical influence of the Leeuwin Current on this important fishery is through its impact on the biology of the lobster at the Abrolhos Islands. In this location, the lobster stock matures at a smaller size than on coastal reefs, and spawns before reaching the minimum legal size for capture (C.F. Chubb, unpublished). The lobsters at the Abrolhos Islands account for about half the annual egg production (C.F. Chubb, unpublished) from the total stock, and are critical for the ongoing productivity of the fishery. While the specific effect of the Leeuwin Current on the spawning stock has yet to be precisely determined, evidence from aquarium experiments has shown that elevated water temperatures, such as those caused by the current at the Abrolhos Islands, increase reproductive activity (Chittleborough 1976). A further important aspect of the fishery involving the Leeuwin Current is the effect on catchability of the lobsters through the influence on temperature and salinity. Furthermore, Morgan (1974) has shown that both temperature and salinity variations at the Abrolhos Islands, (again related to the current), have significant effects on the catchability of the rock lobster. Thus, the Leeuwin Current has a major influence on most stages of the life history of the lobster and the catch ultimately achieved by the fishery (Phillips 1986).

Saucer scallop fishery

The distribution of the saucer scallop (*Amusium balloti*) extends considerably further south on the western coast of Australia than on the eastern coast. On the western coast it extends as far south as 35°S (off Albany) and east along the southern coast to Esperance (122°E) (Gwyther *et al.* 1991), whereas on the eastern coast it extends only as far as 27°S (Moreton Bay) (Dredge 1985). This extension of the range on the western side of the continent almost certainly results from the warming influence of the Leeuwin Current.

Scallop populations throughout the world are acknowledged as having highly variable recruitment as a result of the influence of environmental factors (Caddy 1989). In the Shark Bay scallop fishery catches of *A. balloti* have shown a greater than five-fold variation over the period 1983 - 1990, primarily as a result of inter-annual variations in recruitment (Joll & Caputi 1991). Examination of satellite imagery of Shark Bay suggested that the Leeuwin Current may be the environmental factor responsible for this recruitment variation. The imagery showed tongues of warmer water, derived from the south-flowing Leeuwin Current, entering the bay during the spawning season (April to December (Joll 1987)) and possibly affecting recruitment. Populations at locations further south (*eg* the Abrolhos Islands) spawn at different times of the year (Joll 1989) and are probably less vulnerable to any environmental influences of the Leeuwin Current.

Surveys to measure recruitment in Shark Bay have been conducted in November each year since 1983. Growth data from tagged scallops (Joll 1987) showed that scallops from size classes as small as 30-39 mm in November reach a size of around 90 mm by March of the following year, at which size they are acceptable for commercial harvest. Trawling surveys in November, therefore, are capable of estimating the abundance of recruits from the current spawning season which will reach sizes appropriate to enter the fishery in the following year.

Data on landings of scallops by vessels operating in the scallop fishery are provided voluntarily by fishermen in their research logbooks and these are checked against wholesale buyers' receival records. In all years except 1983 the fishery has ceased before the legal closing date when catches have fallen to levels which are not commercially viable. With the exception of 1984, therefore, the catch in each year has been dominated by the new recruits from the previous year's spawning.

The strength of the Leeuwin Current is reflected in the coastal sealevel (Reid & Mantyla 1976, Pearce & Phillips 1988), so that data from the Fremantle tide gauge are a useful index of the flow of the Leeuwin Current. The sealevel at Carnarvon may have more accurately reflected the influence of the Leeuwin Current in the Shark Bay area, but these data were not available for the whole of the period of this study.

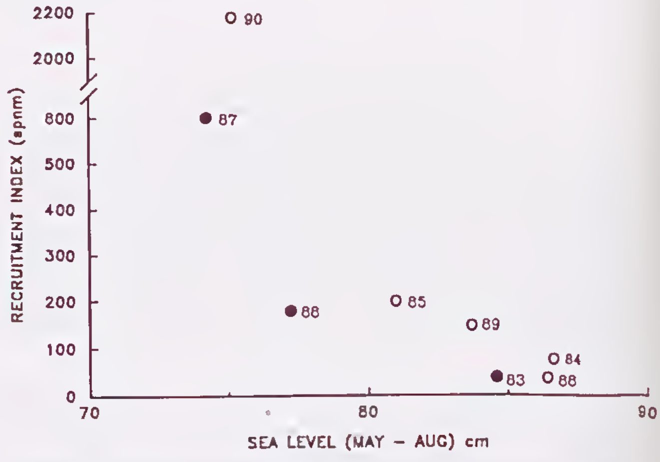

Figure 8 Relationship between the recruitment index for saucer scallops (*Amusium balloti*) in Shark Bay over the period 1983 - 1990 and the mean sealevel at Fremantle over the period May to August of the same year. (83 = year of data; ● ENSO years; ○ Non-ENSO years) (spnm = scallops per nautical mile).

Spawning activity, which results in recruits detectable in the November survey and which subsequently contribute to the recruitment to the fishery in the following year, occurs mainly in the period, April to July (Joll & Caputi 1991). Therefore, in considering the effects of the Leeuwin Current on scallop recruitment, it is the strength of the current in

these months which is likely to be of greatest importance. As the peak in the sealevel at Fremantle due to the current occurs about a month after the peak at Carnarvon, the sealevel over the months of May to August at Fremantle was used as the environmental variable to examine the influence of the Leeuwin Current on spawning / recruitment success in Shark Bay over the period April to July.

Over the period 1983-1990, average Fremantle sealevel for the months May to August was negatively correlated with the abundance of recruits measured in the November survey of that year (Fig.8). Similarly, there was a negative correlation between the Fremantle sealevel over the months May to August and the catch of the fishery in the following year (Fig. 9). The catch for 1991 indicated in Fig. 9 is a conservatively estimated figure based on the very high recruitment index recorded in November 1990. By the end of June 1990 the catch of the fishery was over 1 000 tonnes.

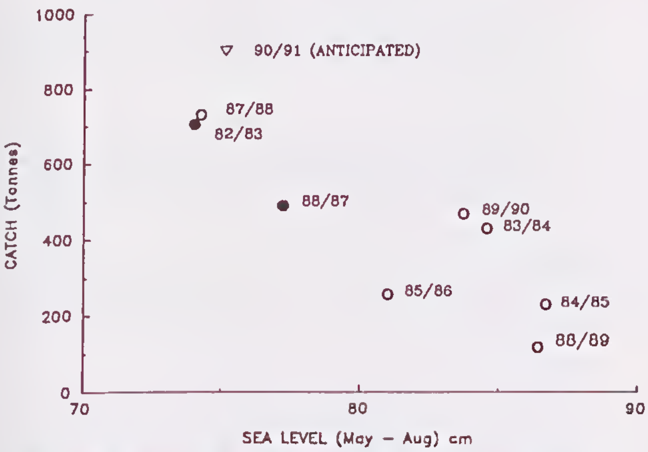

Figure 9 Relationship between the annual catch of saucer scallops (*Amusium balloti*) from Shark Bay over the period 1983 to 1991 and the mean sealevel at Fremantle over the period May to August of the previous year. (83/84 = year of sealevel data / year of catch data; ● ENSO years; ○ Non-ENSO years). (1991 catch data are anticipated).

The mechanism by which the Leeuwin Current influences recruitment success in *Amusium balloti* in Shark Bay has not been determined. However, the data suggest very strongly that in years of a weak Leeuwin Current, both recruitment success and the catch in the following year will be high. The Leeuwin Current is known to be weakest when El Niño/Southern Oscillation (ENSO) events occur (Pearce & Phillips 1988), so that good recruitment could also be expected to be associated with these events. Massive increases in the abundance of the Chilean scallop (*Argopecten purpuratus*) were noted to be associated with the ENSO event of 1982/83 by Arntz (1984) and Wolff (1987).

While the mechanism of action of the environment on recruitment success of *Amusium balloti* has not been positively identified, hydrological flushing in years of strong Leeuwin Currents seems a strong possibility. Both Dickie (1955) and Caddy (1979,1989) noted the importance of hydrological flushing in recruitment success of the Atlantic sea scallop (*Placopecten magellanicus*). Strong Leeuwin Currents also bring warm, low-nutrient waters into Shark Bay. Thus, other possibilities for the mechanism of action may be negative effects of increased temperatures on spawning or the success of fertilization or a reduction in primary production leading to an inadequate food supply for the larvae. Whichever mechanism or combination of mechanisms is responsible for the observed influence of the Leeuwin Current, it is clear that the effect of the current is to depress fisheries production in an embayment which is otherwise capable of high productivity.

Penaeid prawn fishery of Shark Bay

The largest Western Australian fishery for western king (*Penaeus latisulcatus*) and brown tiger (*Penaeus esculentus*) prawns is located in Shark Bay (Penn *et al.* 1989), a sector of the coast frequently influenced by the Leeuwin Current.

The current has two major effects on the prawn fishery particularly the major western king prawn stock. It firstly radically changes the annual temperature cycle on the trawl grounds (Penn 1988) from that found in the more usual annual cycle in inshore waters which are unaffected by the current. The winter Leeuwin Current flow results in the temperature of the shelf water peaking later, usually in May; and a period of lower temperatures extending through spring, when the warm current declines and cooler local inshore waters dominate. This unusual temperature regime alters the burrowing behaviour of western king prawns (Penn 1984) and thereby influences the catches of prawns. The resulting changes in catchability produce high catches and maximum exploitation rates from the start of each season in March through to May/June of each year, followed by significantly lower catches and exploitation rates for the remainder of the year. Alterations in the annual temperature cycle, particularly the timing of the temperature decline in May/June that is almost certainly related to the timing of the current peak, have been simulated in a computer model (N.G. Hall & J.S. Andrews, pers. comm.) which predicts catch variations in the order of 20% with a one month alteration in the time of the temperature decline.

Secondly, within each season, there is also a significant correlation (r=0.6) between recruitment catches each year, and the strength of the Leeuwin Current expressed as the mean monthly Fremantle sealevel over the period April to August of that same year. Since the spawning season for king prawns recruited in a particular year is during winter/spring of the preceeding year, the above correlation suggests that the current is having an effect on the survival, or

growth, of recruits, once the year class has migrated out into the main trawl ground in the northern region of Shark Bay (Penn *et al.* 1989).

As a result of the generally positive relationship between the current strength and prawn catches, and the negative effect of the current on the scallop recruitment to the same trawl fishery, the cycles in prawn and scallop catches are often out of phase. Furthermore, the relatively infrequent occurrence of weak Leeuwin Current years results in consistent, relatively large king prawn catches and on average low scallop catches with occasional very high catches resulting from strong recruitment.

Summary

In conclusion, under the influence of the Leeuwin Current, a more tropical coastal water environment has evolved off south-western Australia. This situation contrasts markedly with those of other environments characteristic of eastern boundary currents. The oceanic sources of nutrients which support extensive plankton-based food chains on other western continental shorelines where upwelling occurs are not available off Western Australian. Fisheries production in these waters is therefore heavily dependent on benthic-based food webs in near-shore waters, rather than on those associated with oceanic ecosystems.

Thus inshore demersal invertebrate fisheries such as rock lobster, rather than pelagic finfish resources, dominate fisheries production in Western Australia.

Both the strength and timing of the peak current flow also appear to influence significantly the annual catches of most of the economically important finfish and invertebrate resources of the west and south coasts of Western Australia. Depending on the species being considered, strong current flows can either adversely or favourably affect catches. The precise mechanisms however, are in many instances still poorly understood, although larval dispersal and catchability variations are thought to be the most likely factors.

Long-term studies into the important interaction between the Leeuwin Current and Western Australia's major fisheries are ongoing with a view to increasing the level of understanding of the mechanisms underlying the effects of the current.

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Coral reefs in the Leeuwin Current - an ecological perspective

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Abstract

The Leeuwin Current differs markedly from other eastern boundary currents in that it transports tropical water towards a polar ocean, and inhibits upwelling. As a result, the offshore marine environment of Western Australia is characterised by elevated sea temperatures and reduced dissolved nutrient and particulate concentrations relative to adjacent coastal and south-west Indian Ocean water masses. As in many western boundary currents, the distribution of coral reefs in and near the Leeuwin Current is extensive, and appears to mirror the influence of the current, with the limit of active reef accretion offshore extending well outside the tropics. Causality in the relationship between the regional oceanography and coral reef development has not been established, but the assumed dominance of sea temperature as a factor controlling reef growth is questioned on the basis of the evidence available. The Leeuwin Current's role in maintaining apparently low rates of nutrient delivery to the benthos, in combination with its elevation of sea temperature and advection of planktonic spores and larvae, serves to inhibit the development of marine macrophyte communities, which compete effectively with coral reef-building communities. At reefs where these two benthic community types overlap (*ie* the Houtman Abrolhos), periodic delivery of high nutrient water is inferred by the extent of non reef-building macrophyte communities. I suggest that the primary influence of the Leeuwin Current on coral reef development is to modulate the competition between coral and macrophyte communities. More oceanographic measurements, geological analyses and ecological experiments are required to test the hypothesis.

Introduction

The role of the Leeuwin Current in controlling the development and distribution of coral reefs along the Western Australian coast has been a subject of interest at least since Saville-Kent's (1897) observations of the Abrolhos reefs. There has also been a great deal of speculation on the topic, and precious little hard data collected. In this brief review I will make limited comparisons between the Leeuwin and other current systems, and discuss the most obvious mechanisms by which ocean currents may control reef growth. Finally, I will focus on the Abrolhos as the epitome of Leeuwin Current reefs.

Clear definition of terms is required. I have followed Fagerstrom (1987) in defining coral reefs as: "carbonate structures with a framework dominated by the skeletal remains of zooxanthellate, scleractinian corals, supporting a living veneer of those and other calcifying organisms". This definition encompasses the majority of photic zone, Holocene reefs, but specifically excludes aphotic zone reefs dominated by hermatypic corals, non-coral dominated reefs (*eg* algal-millepora reefs), and communities of corals living on non-coral reef structures such as limestone or sandstone.

The Leeuwin Current is well defined by Cresswell & Golding (1980), Thompson & Veronis (1982), Godfrey & Ridgway (1984), and by Pearce (1991) in this volume. It is a narrow (<200 km), shallow (<200 m) stream of relatively warm, low salinity, low nutrient oceanic water of tropical origin which flows southwards at relatively high velocity (0.1 - 0.4 ms^{-1}) along the western continental slope of Australia. The Current is driven by a latitudinal gradient of steric sealevel, is seasonal in its volume flux and sheds large and mesoscale eddies into the Indian Ocean and onto the shelf. The stream is coherent at least from North West Cape to Cape Leeuwin, with clear influence on flows on the Northwest Shelf and in the Great Australian Bight. I refer to this extent of continental shelf and slope as the "Leeuwin Province".

Coral Reef Initiation and Accretion

Extant coral reefs in the Leeuwin Province began growth within the past ten thousand years as coral communities recruiting to newly available marine substrata during the Holocene transgression. The basement could be either a former coral reef, killed during a glaciation perhaps, or any other hard surface in shallow water. Under suitable conditions reefs grew upwards at rates which approximated the rate of sealevel rise. Those which reached the sea surface then expanded horizontally.

Figure 1 Chart of the earth between the 40° parallels, showing the major boundary currents, the 18°C winter minimum monthly mean isotherm. and the distribution of coral reefs (modified from Neumann & Pierson 1966, Veron 1986). Boundary Current codes: A.C.= Agulhas Current, B.C.= Brazil Current (off S.America) & Benguela Current (off Africa), C.C.= California Current (off N.America) & Canary Current (off Africa), E.A.C.= East Australia Current, G.C.= Guiana Current (off S.America) & Guinea Current (off Africa), G.S.= Gulf Stream, K.S.C.= Kuro Shio Current, L.C.= Leeuwin Current, M.C.= Mozambique Current, P.C.= Peru Current (Humbolt Current). Latitudinal limits of coral reefs in the open ocean are indicated by doubled-ended brackets, those near coasts by single-ended brackets.

The essential dimension of reef growth is time. With upward accretion rates ranging from 1 to 10 mm per year, even modest reef structures represent temporal integration of environmental controls over thousands of years. Perhaps the single strongest message from oceanographic research during the last decade has been the variability of even the largest ocean structures. Rapid, glacially-forced change in sealevel is the penultimate control on patterns and rates of coral reef development (Davies & Montaggioni 1985). The ultimate control is the foundation upon which photic zone reefs must rest. Coral reefs cannot develop even under ideal atmospheric and seawater conditions if they have no structure within the upper 100 m of the ocean upon which to initiate growth.

The lack of shallow foundation is not a constraint on the shallower portions of the continental shelves off Western Australia, but is absolute on the shelf slope where the Leeuwin Current flows. The dearth of tectonism and related seamounts and guyots means that there are few potential reef sites actually in the Leeuwin Current: most are on the adjacent shelf or coast.

Even when the foundation of a Leeuwin reef is of coral construction, historical interruptions in vertical accretion of sufficient duration may have precluded subsequent reef development. The world's oceans are littered with the ghosts of drowned reefs, overlain by a photic zone ideal for coral growth (Menard 1986). Who knows what ghosts lie beneath the Leeuwin Current?

The process of reef accretion is the net result of a coral community's initiation and subsequent development in a particular environment. It requires:

1) A consistent supply of the larvae of reef-building, binding and infilling plants and invertebrates, most of which have a planktonic life stage. The supply can be from both local populations (*ie* self-seeding) and from distant reefs. Such immigration is a requisite for initial reef colonization.
2) Suitable substrata for larval settlement when they are delivered to a region: there must be available space on the seabed within the photic zone.
3) Suitable environmental conditions for the survival and growth of newly settled recruits through to the adult life stages, including:
   a) Non-lethal sea temperatures and salinities.
   b) Adequate irradiance for positive net daily photosynthesis by symbiotic and free-living algae.
   c) Adequate supplies of inorganic nutrients to meet the demands of autotrophic organisms for growth and calcification.
   d) Low concentrations of inorganic and organic particulates in the water column which otherwise inhibit coral growth by shading, smothering, and promoting bacterial infection.

Clearly many of the requirements for coral reef accretion such as temperature, light and nutrient concentration are the very factors which are strongly influenced by regional oceanography such as boundary currents. Poleward-flowing boundary currents, including the Leeuwin Current, have the potential to influence all of these factors, either directly or indirectly. The transport of tropical reef larvae and moderation of winter sea surface temperatures have received most attention. What can we learn about the Leeuwin's influence on coral reef development by looking at the global distribution of boundary currents and reefs?

Boundary Currents and Reef Systems

The global distribution of coral reefs as defined here is quite predictable (Fig.1). Reefs occur exclusively within the photic zone, and usually within 18°C mean monthly minimum isotherm. In the open oceans the latitudinal limits of reef development fall close to the tropics, generally within the 25th parallels (*eg* Midway in the north Pacific). Within semi-enclosed seas (*eg* Red Sea, Persian Gulf) and ocean margins however, the isotherms are distorted by continental influences and deflection of currents which close the great ocean circulations. Western boundary currents are the strongest, carrying warm water poleward in relatively narrow and deep streams such as the Mozambique - Agulhas Current system of eastern Africa. This current extends the poleward limit of reef development to well south of Durban (Fig.1).

On the eastern margins of the ocean basins the westerly flows of the major gyres are deflected towards the equator in slower boundary currents which are usually broad and shallow (Fig.1). Because of Coriolis' force and the trade winds, eastern boundary currents are generally characterized by upwelling at their coastal edges. Thus, the Benguela and Peru Currents are the analogs of the West Australian Current, and should serve as comparative models for the distribution of coral reefs in eastern boundary currents.

Such a comparison will perforce be brief. Only three reef systems (including the Galapagos) fall within the precinct of the Peru Current, the southernmost of which is at only 7°S near the coast at Chiclayo, Peru (Fig.1). All of them, including those at the Galapagos Islands over 1000 km from the South American coast, are marginal reefs in terms of their extent, diversity and vertical accretion rates. Coral reefs in the Gulf of Guinea at the northern extreme of the Benguela Current extend only 2°S of the equator.

It is apparent that the cold, nutrient-rich waters of eastern boundary currents somehow inhibit the development of coral reefs. Presumably, that is one reason why there are no open ocean atolls on the few seamounts in the West Australian Current. In contrast, the Elizabeth and Middleton Reefs occur at 29 to 30°S near Lord Howe in the East Australian Current.

The Leeuwin Current is clearly not a typical eastern boundary current. Its high poleward velocity and narrowness liken it to a western boundary current. But it is differently forced and shallower, so it moves a far smaller volume of water. In some ways it resembles the narrow currents which interpose between the major boundary currents and the coasts off North Africa and the America's, such as the Guinea Current and the Labrador Current extension. Both of these are equatorward currents, however, and are not strictly comparable with the Leeuwin.

As an oceanographic feature, the Leeuwin Current appears to be in a class by itself. The distribution of reefs along the Current, however, is repeated in poleward flowing boundary currents throughout the world. In terms of the factors controlling the development of coral reefs, more appropriate comparisons might be made with western boundary currents such as the Agulhas Current, the East Australian Current, the Kuro Shio Current and the Antilles/Florida/Gulf Stream current system. Like the Leeuwin Current, all of these sustain coral reefs in decreasing density and diversity along gradients through the tropics to well beyond them at Durban, Lord Howe Island, Kyushu Island and Bermuda respectively. They originate in regions rich in coral reefs and thus can transport reproductive propagules in a conducive biophysical regime.

Hydrologic Factors and Reef Growth

Space does not permit extending the comparisons in further detail here, but there is something to learn from examining parameters of reef structure and function along latitudinal gradients, and among boundary current systems. The major conclusion I draw is that while temperature alone is a reasonably good correlate of reef distribution, there are enough exceptions to the 18° 'law' (Wells 1957) at high latitude coral reefs to reject temperature as the sole factor limiting reef development.

The apparent correlation of coral reef distribution with minimum ocean temperatures (Fig.1) has led to the assumption of causality (Dana 1843, Rosen 1971, Burns 1985). The physiological data for individual coral species is far from conclusive. Corals and algae exhibit a high degree of plasticity in their responses to temperature extremes (reviewed in Brown & Howard 1985, Hatcher *et al.* 1989), and extrapolations from species-specific responses of local populations to reef building communities is problematical. Certainly instances of extensive natural mortality resulting from thermal stress have been documented (*eg* Shinn 1976, Roberts *et al.* 1982, Burns 1985), but active reef growth has been documented in environments where minimum mean temperatures extend well below 18°C (*eg* Downing 1985, Tribble & Randall 1986, Coles & Fadlallah 1991), and some species of hermatypic corals survive in temperatures as low as 11°C (*eg* MacIntyre & Pilkey 1969, Veron & Marsh 1988).

Identification of causality in controls on reef growth is complicated by the correlation of temperature, salinity, irradiance, nutrient and particulate gradients along geographic axes such as latitude and proximity to shore. Gradients of increasingly unsuitable environmental conditions for reef growth are characterized by a decrease in coral abundance and diversity, and an increase in the abundance of macroalgae (particularly Phaeophytes) at higher latitudes and close to continental land masses

(Johannes *et al.* 1983a, Birkeland 1988, Coles 1988, Sheppard 1988). Studies of reefs in the middle of this transition (*ie* supporting both coral and macrophyte-dominated communities) have led to the conclusion that competition for space, light and nutrients between these two groups of benthic organisms is an important factor controlling the development and distribution of coral reefs near the poleward and landward ends of gradients (Johannes *et al.* 1983a, Hatcher 1985).

Complex (often non-linear) interactions amongst water quality parameters (*eg* nutrient concentration, turbidity, temperature) render the comparative approach of observing reef structure and performance along gradients inconclusive. For example, neither Liddell & Ohlhorst (1988) nor Sheppard (1988) were able to unequivocally identify the determinants of declining reef development along geographical axes in the Western Atlantic or Arabian Gulf regions from synoptic comparisons of coral abundance and diversity. Clearly, no single factor controls the transition from coral reef to kelp bed. Rather, the total environment must be considered in terms of its effects on the competitive abilities of the pool of available benthic organisms. Oceanographic conditions exert major, but not exclusive controls, on this environment.

Coastal runoff and its accompanying sedimentation have great potential to modify the influence of boundary currents on reef distribution and development, because of their strongly negative effects on coral growth and survival (reviewed in Birkeland 1988, Hatcher *et al.* 1989). The arid conditions of Western Australia modify the influence of the Leeuwin Current on reef development along the coast to a lesser extent than, for example, the wet coast of east Africa modifies the influence of the Agulhas Current.

Examination of the distribution and structure of coral reefs influenced by the Leeuwin Current reinforces the conclusions drawn above.

Coral Reefs of the Leeuwin Province

Four major and two minor coral reef systems fall under the influence of the Leeuwin Current (Fig.2, Table 1). From north to south they are:

1) The Rowley Shoals,
2) The Dampier Archipelago & adjacent reefs of the Pilbara coast,
3) The Ningaloo reef tract and adjacent reefs,
4) The western islands of Shark Bay,
5) The Houtman Abrolhos reefs and adjacent banks, and
6) The Pocillopora reef at Rottnest Island.

With the probable exception of the Rowley Shoals, all of the Leeuwin reefs were high and dry at the start of the Holocene transgression 10,000 years ago. Their colonization and growth is a geologically recent event.

It is important to be precise about the definition of a coral reef in this context. Isolated coral colonies, or spatially restricted groups of corals, and their associated epi- and infauna extend at least as far south as Cape Naturaliste. They do not form the vertically or horizontally accreting structures of coral framework, infilled and cemented by detritus and algae, which are here defined as coral reefs. It is quite possible that there are other small reef structures fringing the coast between Northwest Cape and Perth (*eg* Point Quobba, just north of Shark Bay, Veron & Marsh 1988) which would meet these criteria, but they have not been described adequately. Knowledge of such reefs would be useful in separating coastal from Leeuwin Current influences on coral reef development.

The four reef systems differ markedly in their physiography, geology and degree of interaction with the Leeuwin Current.

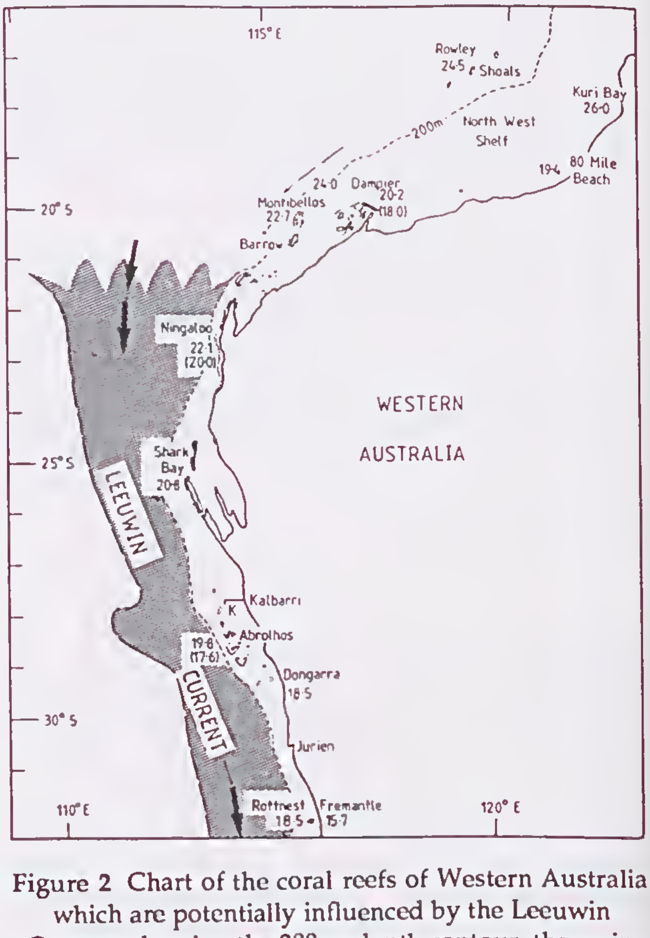

Figure 2 Chart of the coral reefs of Western Australia which are potentially influenced by the Leeuwin Current, showing the 200 m depth contour, the main stream of the Current, and the northern limit of kelp (*Ecklonia*) occurrence (K). Minimum mean monthly sea surface temperatures are shown in °C for reef and coastal locations, with absolute minimum values recorded in brackets (from Veron & Marsh 1988).

Table 1.

A comparison of relevant attributes of coral reefs of Western Australia which potentially fall under the influence of the Leeuwin Current.

Diversity = # genera/# species, N/D = No Data, Extreme lower temperatures in brackets.

Reef system	Reef Type	Lat. °S	Dist. from Coast km	Dist. between Reefs km	Surround Depth m	Dist. from Slope km	Min. mean Temp °C	Water Quality	Best coral Growth	Abundnt Macro-Algae?	Coral Diversity
Rowley Shoals	Atoll?	17	250-300		200-400	0	24.5	Oceanic, Tidal	Slopes & E. lagoons	No	52/180
				300							
Dampier Archr.	Fringe	20	5-25		10-20	75-100	20.2 (18.0)	Coastal, Tidal	NW. slopes	Yes	57/216
				120							
Monte-bellos	Fringe	20.3	80-120		30	25-40	22.7	Shelf, Tidal	W. slopes	No	30/66
				10							
Barrow Island	Fringe	20.5	60		25	60	N/D	Shelf & Coastal	W. shore	Yes	15/25
				120							
Ningaloo Tract	Fringe/ Barrier	21-23	0.2-7		15	8-50	22.1 (20.0)	Oceanic & Shelf	Flat & Lagoons	No	54/203
				100							
Shark Bay	Fringe	24-26	0		25	60-80	N/D	Shelf & Coastal	W. shores	N/D	28/82
				250							
Houtman Abrolhos	Plat-form	28-29	45-70		30-40	10-20	19/8 (17.6)	Oceanic & Shelf	E. slopes & Lagoons	Yes	42/184
				330							
Rottnest Island	Fringe	32	20		15-30	20-30	18.5	Shelf & Coastal	S. shore	Yes	16/25

The Rowley Shoals

The Rowley shoals are shelf-slope platform reefs of classic structure and development (Fairbridge 1971). As such, they probably represent a long history of reef growth, with a relatively thick, coral-rich Holocene stratum on the Pleistocene reef basement (Berry 1982). Their position, 700 km northwest of what is generally depicted as the northern limit of the Current at Exmouth (*eg* Pearce & Cresswell 1985), begs the question of their classification as Leeuwin reefs. Currents on the Northwest Shelf, however, exhibit a distinct SW component which is coherent with the Leeuwin Current flow further south (Holloway & Nye 1985), suggesting that this area forms part of the headwaters of the Current. Eastward flowing water from the northern Indian Ocean (and perhaps a southwestward flow from the Timor Sea) undoubtedly bathes the Rowley Shoals as it assembles for its rush south along the shelf slope in the Leeuwin Current.

The Dampier Archipelago & adjacent reefs of the Pilbara coast

A similar generalization applies at least to the outer portions of the Dampier Archipelago and adjacent Lowendal, Monte Bello and Barrow Islands, which occupy the inner, southeast portion of the Northwest Shelf. The coral reefs comprise an extensive array of small, barrier and fringing reefs growing in shallow water adjacent to hundreds of small continental islands (Simpson 1988). They are primarily Holocene structures, resting on non-reefal basements of continental rock. A large range of reef habitats, from high energy, coral covered outer reef slopes to stagnant, depauperate lagoons is the result of this geographic diversity (UNEP/IUCN 1988).

From about February to June the currents on the shelf adjacent to these reefs are predominantly southwest (Mills *et al*. 1986). The source of the water in these currents is unclear, but its quality is strongly influenced by benthic resuspension and runoff from

the adjacent coast (Simpson 1988). Whether it is considered part of the Leeuwin Current or not, much of the water flowing through these reef systems during that period soon joins the Current off Exmouth.

The Ningaloo reef tract and adjacent reefs

The Leeuwin Current is a clearly delineated entity at the Murion Islands off the north end of the Ningaloo reef tract. Australia's largest fringing reef system is separated from the arid coast by only 0.2 to 7 km of shallow lagoon. The best coral reef development occurs in reef passes and within this lagoon. Although the shelf is narrow here, the outer reef slopes are not characterized by rich coral communities extending to great depth, as found, for example at the Rowley Shoals. It appears that the underlying structure of the reef below about 10 m depth is not a Pleistocene reef matrix, but rather a mixture of aeoleanites, calcarenites and tertiary limestones supporting very few corals (May *et al.* 1983, Veron & Marsh 1988, UNEP/IUCN 1988). The Ningaloo Reef tract is likely to be a thin layer of coral matrix built on old coastal features during the Holocene transgression, rather than an ancient coral reef. Perhaps reduced precipitation during the Holocene allowed the reef to grow closer to shore than had been possible during previous interglacial periods.

Having made statements about the structure of Leeuwin reefs, I emphasize that it is impossible to be certain about their underlying composition because no coring has been done. The holes currently being sunk at the Abrolhos (see Collins *et al.* 1991) should fill a major gap in our knowledge.

The pattern of circulation within the Ningaloo reef lagoon ensures rapid exchange with the waters immediately adjacent to the outer reef edge (Hearn *et al.* 1986). There are few oceanographic data from outside the reef, but the proximity of the shelf break (Fig.2) strongly suggests that the Leeuwin Current is the major reservoir for lagoonal exchange.

Shark Bay

Narrow fringing reefs partially line the seaward edges of the islands which form the western boundary of Shark Bay. The islands separate the high salinity water of this large inverse estuary from the shelf waters, and the corals are best developed on their seaward margins (Veron & Marsh 1988). Because there has been little documentation of the biota or physical environment of these reefs, it is difficult to assess the influence of the Leeuwin Current on them. The continental shelf is over 100 km wide at this latitude, however, so the potential influence of the Leeuwin Current is likely to be attenuated.

The Houtman Abrolhos reefs and adjacent banks

On the edge of the shelf between 28 and 29°S latitude lie a series of submerged and emergent reefs which often receive the full force of the Leeuwin Current (Fig.3). While undeniably the products of coral accretion over geological time periods, the Houtman Abrolhos Reefs are unlike any other Australian reef system in morphology and community structure (Saville-Kent 1897, Veron 1986). A Holocene coral veneer is virtually non-existent on the western, that is, seaward portions of the reef platforms. Instead, there grows an unusual mixture of macroalgae of temperate and tropical affinities (Hatcher 1985, Hatcher *et al.* 1987). Yet the relicts of classic spur and groove topography, symptomatic of healthy reef accretion in high energy environments, are evident.

In the eastern portions of the platforms extensive and diverse accumulations of Holocene coral matrix dominate what is clearly a severely eroded Pleistocene reef topography. In places like Turtle Bay in the Wallabi Group, the Pleistocene reef structures are exposed to reveal rich coral sequences (Teichert 1947, Collins *et al.* 1991).

Several shoals and banks are located on the shelf and slope both to the north and south of the Abrolhos (Figs.2 & 3). To what extent these represent extant or extinct coral reef structures is unknown.

The Leeuwin Current rides the slope 10 to 20 km west of the Abrolhos Reefs, and there appears to be a persistent, large scale (100 + km) cyclonic eddy in the current at this latitude (Fig.2). Sporadically, the warm waters of the Current flood the shelf edge around the Abrolhos, while at other times it forms a narrow jet well to the west (Pearce & Griffiths 1991, Pearce *et al.* 1991).

Rottnest Island

The inclusion of Rottnest Island in a classification of coral reefs is debatable. Most corals on this continental island 20 km off the coast near Perth exist as solitary colonies resting on the submerged limestone platforms which surround the Island (Hodgkin *et al.* 1959). In this respect it represents coral communities found on the coast from Jurien Bay, 150 km north of Rottnest Island, to as far south as Cape Naturaliste and Esperance. Pocillopora Reef, on the south coast of Rottnest Island, is a coral reef structure of about 3 m maximum relief which is dominated by the one species, but which supports many other tropical invertebrates and fish. As such, it meets the minimum criteria of the reef definition used here. It is unlikely that the underlying structure is a Pleistocene reef matrix. A relict coral reef of late Pleistocene age outcrops on the south coast of the Island nearby at Fairbridge Bluff (Playford 1988). It appears to represent a thin but extensive sequence of coral matrix now obscured by non-reefal, Holocene deposits, and indicates that conditions suitable for coral reef development here are not restricted to the recent past.

Rottnest Island is not as proximal to the course of the Leeuwin Current as are the Abrolhos Reefs, but the presence of the Current is evident in sea surface

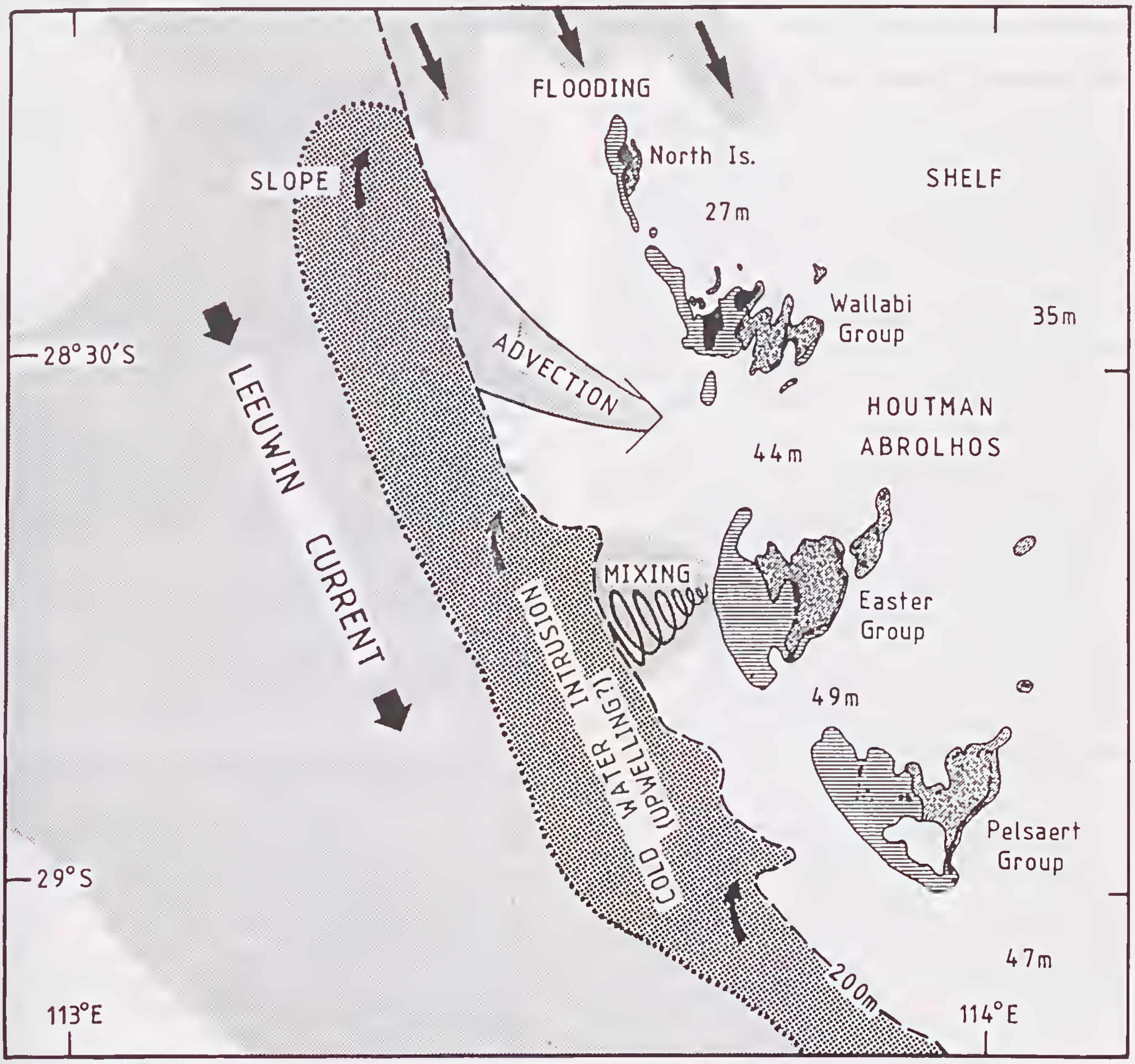

Figure 3 Chart of the Houtman Abrolhos, showing the three major reef platforms (island groups), the 200 m depth contour and representative shelf depths, and generalized circulation features (based on analysis of NOAA-AVHRR imagery, Pearce *et al.* 1991). Areas of subtidal reef dominated by macroalgal communities (horizontal lines) and coral communities (diagonal shading) surround the islands (solid black). Three mechanisms by which Leeuwin Current water (light stipple), and upwelled or intruded water (dark stipple) can influence the reefs on the shelf are depicted.

temperatures and the local hydrography (Pearce *et al.* 1989).

Inter-reef comparisons

Comparison of the salient features of these reef systems (Fig.2, Table 1) reveals several interesting generalizations about the relationship between coral reefs and the Leeuwin Current. With the possible exception of the northern extremity, where temperatures increase shorewards towards Broome, the Leeuwin Current maintains warmer sea surface temperatures at offshore reefs than on the adjacent coast. South of Shark Bay, winter temperatures near the coast often go below 18°C in August or September. The absolute minimum values are generally about 2°C colder (Table 1): for the most part this is a patchy data set, requiring cautious interpretation. I suggest that the offshore and coastal means at the same latitude are significantly different, but that the ranges usually

overlap. The lack of coastal reef development south of Shark Bay suggests either that it is only the mean (rather than the extreme) temperature that matters, or that factors other than temperature are at work.

The reefs of the Leeuwin Province may be divided into offshore and coastal groups, the criterion being distance from the shelf break, rather than distance from the coast. The critical distance appears to be about 50 km from the 200 m depth contour (Table 1). Coastal reefs only occur north of the Abrolhos, and are characterised by more turbid water and greater macroalgal abundance than those offshore. This distinction is most apparent in a comparison between the Monte Bello Islands, which have low macroalgal cover and twice the coral diversity of the reef on nearby Barrow Island, which has abundant macroalgae (UNEP/IUCN 1988).

There is considerable evidence to demonstrate that the presence of macroalgae inhibits coral settlement, growth and survival (Johannes 1975, Crossland 1981, Hatcher 1985). Unlike offshore reefs to the north of Shark Bay, those at the Abrolhos support luxuriant macroalgal communities, including the kelp *Ecklonia radiata* (Hatcher *et al.* 1987), which has its northern coastal limit near Kalbarri (Fig.2). Proximity to the coast, and all it implies in terms of water quality and biotic communities, must thus be seen as another gradient of Leeuwin Current influence, in addition to the more obvious latitudinal cline.

The Role of the Leeuwin Current

Coral reefs are surface phenomena, and as such are particularly influenced by shallow circulations like the Leeuwin Current. Coral reefs are also multidimensional structures which cannot be classified on any single axis. In attempting to interpret the relationship between the Leeuwin Current and its reefs, the multiplicity of factors which interact to control reef structure and development precludes simple cause and effect assumptions in the absence of experimental data. Virtually all of the data available at present are either circumstantial or correlative.

In its simplest guise, the role of the Leeuwin Current in maintaining coral reefs on the coast of Western Australia can be viewed as the flux balance between southern Indian Ocean water derived from the West Wind Drift, and tropical water delivered by the Leeuwin Current. Where mixing is weak and Leeuwin flows dominate, conditions for reef development are good. Where mixing is rapid and Leeuwin flows are diluted and dissipated by their interaction with other water masses, conditions are poor. In this context, one expects to see an attenuation of reef development as one moves away from the centre of the Current (*ie* across the shelf towards the coast or out into the Indian Ocean), and as one moves south and the gradients across which mixing processes occur steepen. It would be nice to have a simple mixing parameter which could be used to quantify the relative dilution of Leeuwin water along these longitudinal and latitudinal axes. Thompson's (1987) scaling model of the Current at shelf scale might be a good place to start.

Several hypotheses can be erected concerning the role of the Leeuwin Current in maintaining coral reefs along the coast of Western Australia. I have listed some of the more obvious ones here:

The first might be termed the "Recruitment Hypothesis":

"Advective delivery of the larvae of reef building organisms in the Leeuwin Current replenishes local populations after local extinctions, and maintains populations of reef organisms at sites where they are not reproductively viable."

Given typical drifter transit times in the Current (Cresswell & Golding 1980), and a maximum distance between any two Leeuwin reef systems of just over 300 km (Table 1), inter-reef transport during the larval stages of most reef-building organisms is entirely feasible (Maxwell & Cresswell 1981).

Two other hypotheses deal with the effect of the Current on water quality in and around offshore and nearshore reef systems. The "Advective Influence Hypothesis":

"Direct advection of Leeuwin Current water maintains elevated temperatures and depressed dissolved nutrient and particulate concentrations which favour the growth of coral reef organisms, and inhibits the growth of macroalgal competitors at offshore sites where the seabed intersects the photic zone and the Current."

The "Mixing Influence Hypothesis":

"Mixing of Leeuwin Current water onto the shelf has a similar effect as advected water masses, but it is attenuated by the quality and quantity of coastal water with which it mixes."

The Advection Hypothesis primarily concerns latitudinal variations in reef development, while the Mixing Hypothesis concerns cross-shelf variation

A fourth hypothesis again concerns water quality for reef development at offshore locations: the "Upwelling Inhibition Hypothesis"

"The Leeuwin Current inhibits wind-driven upwelling of colder, nutrient enriched water on the shelf slope and outer shelf. The degree of inhibition is proportional to the magnitude of the Current in relation to the opposing wind-driven flow."

The degree of upwelling along the coast of Western Australia has been a matter of debate at least since Schott's paper of 1933, and the jury is still out. Certainly it is not a pervasive phenomenon, but even sporadic, local delivery of cold, nutrient-rich water to shallow

reefs can have profound effects on community structure and function.

Processes of upwelling and terrestrial runoff which deliver cold and/or nutrient-rich waters to shallow benthos favour the growth of macroalgae, and have been implicated in the inhibition of reef development. The best examples come from temperature and nutrient proxy records in the skeletons of massive coral colonies collected from currently dead or dying reefs in the eastern Pacific. Increased intensity of coastal upwelling resulting from an equatorward shift in the tradewinds during the little ice age (1500-1850 AD) is implicated in the death of a reef tract on the SW coast of Costa Rica some 150 to 300 years B.P. (Glynn *et al.* 1983). Markedly increased surface concentrations of inorganic nutrients from the Equatorial upwelling occurred during this same period at the Galapagos, suggesting greatly reduced El Niño (Panama Current) flows, and a possible explanation for the scarcity of modern corals at this site (Shen *et al.* 1987, Lea *et al.* 1989, Linn *et al.* 1990). On a more recent time scale, isotopic variations in the thickness and density of growth bands in corals from many locations have been correlated with intra and interannual variations in seawater conditions as influenced by local and global (ENSO) oceanography (*eg* Knutson *et al.* 1972, Smith *et al.* 1979, Boto & Isdale 1985, Barnes & Lough 1989, Hudson *et al.* 1989).

Finally, the dissipation and mixing of Leeuwin Current water as it moves south leads to the "Latitudinal Attenuation Hypothesis":

"All of the effects of the Leeuwin Current are attenuated with latitude, such that a gradient of decreasing diversity, abundance, growth rates and interconnectedness of coral reef communities occurs."

A corollary exists in the compressed gradient towards the coast as Leeuwin water is altered by mixing and terrestrial influences.

The last is not really a testable hypothesis, in that Leeuwin Current effects on reef development are confounded by latitudinal variation which is independent of the Current, such as the latitudinal gradient in solar radiation. It is thus important to identify the mechanisms by which observed gradients in coral reef distribution, structure and function along the Western Australian coast are maintained. Three are obvious.

Mechanisms of Leeuwin Current Influence

A gradient of decreasing species diversity of reef building organisms to the south and east is an obvious feature of Leeuwin reefs (Table 1). It is complemented by an increase in the diversity of competing organisms such as kelp. These changes in community structure provide the simplest explanation for the observed decline in the quantity and quality of reef structures along the Leeuwin gradients. Reefs won't develop in the absence of corals to build framework and associated flora and fauna to cement and infill that framework. If we assume that all shallow areas under the influence of the Current have an equal potential for the survival of recruits, then two mechanisms exist to explain the progressive decrease in the reef-building species pool. Either the species have not reached many potential reef sites in the Leeuwin province from some Indonesian source of radiation, because there has been insufficient time for the advective delivery of critical numbers of larvae, or the larvae have all died *en route*.

The first case is unlikely because the dynamics of the Leeuwin Current favour rapid and direct larval advection, the close proximity of its reefs along stream favour larval advection and "island hopping", and there have been at least 6000 years of relatively stable conditions for dispersal. If there are mechanisms which prevent entrainment of larvae in the Current (*eg* spawning at times of reduced or reversed Current flow), they must be very closely tuned to the Current's dynamics. The only data available suggest that biological mechanisms serve to enhance, rather than inhibit, entrainment of coral larvae (Simpson 1991).

In the second scenario gradients in the physical and biotic environment of the Current cause increased larval mortality due to dispersion, thermal stress and starvation in the south and east of the Current stream. This is a more likely mechanism for producing the observed diversity gradients among Leeuwin reefs, but one for which there is little direct data. At the extreme southern end of Leeuwin reef development at Rottnest Island, the recruitment of *Pocillopora* colonies with genotypes differing from adjacent colonies is very patchy in space and time (Stoddart 1984). The recruitment of tropical fish species to Pocillopora Reef is also a rare event compared to tropical reefs (Hutchins 1991), suggesting that depletion of both larval abundance and diversity down the current is an important phenomenon.

If, on the other hand, we assume that reef-building organisms have equal potential for recruitment to shallow locations within the Leeuwin province, then the observed pattern of reef distribution and development is due to variations in post-recruitment growth and mortality. In this case differences among reefs are due to differences in their local physical, chemical and biotic environments. Observed variation in potentially controlling factors such as reduced sea temperature and increased nutrients, particulates and coral competitors southwards and shorewards are strongly influenced by the Leeuwin Current. Gradients in the marine environment, largely maintained by the Current's flow southwards, provide the most obvious mechanism for maintaining gradients in coral reef development along the Western Australian coast.

A third mechanism is variation in habitat diversity. If we again assume that reef-building organisms have equal potential for delivery to all Leeuwin reef sites

(admittedly unlikely), then differences among reefs may be due simply to variation in the range of habitats available for colonization and suitable for accretion at any given site. Habitat diversity is undoubtedly a major determinant of coral species diversity at the scales of individual reefs (Rosen 1971, Veron 1986). There is no evidence, however, for the consistent geographic variation in habitat diversity at the scale of the Leeuwin Current, which would produce the observed patterns of species diversity (Table 1). Indeed, some of the most southerly sites, such as Rottnest Island and the limestone reefs north of Perth, offer extreme habitat complexity, yet support species-poor coral and coral-associated communities (Hodgkin *et al.* 1959, Marsh 1974).

The mechanisms proposed here are not mutually exclusive. Undoubtedly all three operate to some extent in producing the pattern of reef development within the Leeuwin Province. On the available data, it appears that the Leeuwin Current exerts its major influence by maintaining gradients of temperature, dissolved macronutrients and particulate organics which determine the growth and survival of reef-building organisms in planktonic and benthic stages of their life histories, through both direct physiological effects, and indirect competitive (and predation) effects.

Understanding the influence of the Leeuwin Current on the structure and function of its coral reefs is not simply a question of determining effects on the environmental factors which currently control benthic community structure, growth rates and other parameters of existing reefs, although that is a good place to start. Also required is a knowledge of the geological history of their development, both in terms of changes in the Leeuwin Current itself, and changes in global parameters such as sealevel, surface radiation and source pools of colonizer species. Fortunately, while temporally integrating environmental influences on their development, coral reefs also record many of those environmental signals. Our best clues to the past influence of the Leeuwin Current on coral reef development off Western Australia lie within the calcium carbonate matrix of the coral skeletons themselves. This record is only now being exposed (Collins *et al.* 1991, Pearce *et al.* 1991).

The Houtman Abrolhos - Australia's Galapagos

The Houtman Abrolhos epitomize the anomalous ecological consequences of the Leeuwin Current. Southernmost in the Indian Ocean, the Houtman Abrolhos are coral reef communities at the limits of existence, extending, with the help of the Leeuwin Current, well into a region dominated by macroalgal communities. Northernmost in the South Pacific, the macroalgal communities of the Galapagos are at their limits of existence also, extending well into a region dominated by coral reef communities, with the help of the Peru Current and upwelling of the Equatorial Undercurrent. In both archipelagos, coral and macroalgal communities vie for dominance of the substrata, with the outcome apparently dependent on their local oceanography.

One of the most striking and counter-intuitive aspects of the Abrolhos reefs is the lack of vital coral communities on the most characteristic coral-built structures: the windward reef slopes (Fig.3). Clearly, what used to be actively accreting coral structures are now kelp beds (Wilson & Marsh 1979, Hatcher 1985). When did this transition take place? What was the cause of it? Is it an ongoing process? What is its relationship to the structure and dynamics of the Leeuwin Current?

Analysis of NOAA AVHRR satellite images demonstrates that both direct advection of Leeuwin Current water onto the platforms (shelf flooding and cross-shelf streams), and cross-shelf mixing between Leeuwin & shelf water can influence the Abrolhos (Pearce *et al.* 1991, Fig.3). Whatever the mechanism, the portions of the Abrolhos likely to experience the strongest Leeuwin Current influence are the western reef margins and adjacent lagoons: the areas with the poorest reef communities (Fig.3), and no apparent accretion.

In contrast, the eastern margins and lagoons experience more contact with cooler, nutrient enriched coastal water masses moving north along the shelf under the influence of the prevailing winds (Cresswell *et al.* 1989). Yet these portions of the reefs support the richest coral communities south of Ningaloo (Table 1, Fig.3), high community production and calcification rates (Smith 1981), and obvious vertical and horizontal accretion (Wilson & Marsh 1979, Hatcher 1985, Collins *et al.* 1991, Hatcher, unpublished data).

It is possible that the present distribution of corals within the Abrolhos is related to human activities there (Hatcher *et al.* 1990). Perhaps the distribution reflects differences in wave energy. Many of the robust corals which characterise wave swept reef fronts do not occur at the Abrolhos (Veron & Marsh 1988, Veron pers.comm.): have those species simply not been able to survive the trip? There is no evidence to suggest that corals adapted to high energy environments are less capable of dispersion. The alternative explanation is that conditions for the growth of corals on the exposed portions of the Abrolhos reefs are unsuitable for coral growth and survival.

Experimental results demonstrate that macroalgae are able to outcompete corals for light and space at the Abrolhos, particularly in the absence of intense herbivory (Crossland 1981, Johannes *et al.* 1983a, Hatcher & Rimmer 1985, Hatcher, unpublished data). The nutrient concentrations required to maintain high biomass communities dominated by macroalgae are also known to characterize the lagoons and adjacent waters of the Abrolhos reefs (Johannes *et al.* 1983b, Crossland *et al.* 1984, Hatcher 1985). Indeed, nutrient

concentrations at the Abrolhos are the highest ever recorded in an unpolluted coral reef ecosystem (Crossland 1983), averaging 3 to 12 times the mean values in the centre of the Leeuwin Current stream. The concentration gradient is hypothesized to be largely the result of the decomposition of macroalgae advected into the lagoons from the windward reef slopes (Crossland *et al.* 1984, Hatcher 1983, 1985, unpublished data).

While nutrients are effectively sequestered and recycled by the reef systems of the Abrolhos, the efficiency cannot be perfect. New nutrients necessary to maintain the observed macroalgal growth and concentration gradient must be supplied from outside the reef systems at time scales at least approximating the turnover times of the dominant macroalgae: seasonally to annually. Cross-shelf mixing of coastal waters, enriched by terrestrial inputs (Cresswell *et al.* 1989) is a possible source of new nutrients to the Abrolhos ecosystems, but the distribution of macroalgal communities on the reefs argues against it as the major source.

The satellite images occasionally show tongues of cold water off the western margins of the reefs (Fig.3; Pearce, Hatcher & Wyrwoll, unpublished data). If these represent upwelled water, enriched in nutrients from off reef sources, then they could explain the high biomass of macroalgae (including the kelp *Ecklonia*) at these sites. A temperature logger at 5 m depth on the north end of the Western Reef in the Easter Group (Fig.3) records sporadic, several degree drops in sea temperature lasting 2 to 6 days (Pearce & Hatcher, unpublished data). Without simultaneous nutrient data this is not conclusive evidence of upwelling. It is notable that the upper depth limit of *E. radiata* on the western reef slopes at the Abrolhos occurs at about 5 m, while the most luxuriant growth is from 15 to 45 m. Upwelling (or "uplifting" cf. Rochford 1991) on these reef slopes may rarely reach the sea surface.

The case of *Ecklonia* growing on the fringing coral reefs of the coast in the Gulf of Oman provides a fascinating counterpoint to the Abrolhos situation. There the kelp also does not grow above 5 m depth. It has developed an annual growth strategy which is tuned to the well-documented and highly seasonal monsoon-driven upwelling. The nutrient-needy sporophyte is found only during the upwelling period. For the remainder of the year, the plants survive as microscopic gametophytes, and the benthic community looks like a typical coral reef (Barratt *et al.* 1984). In the Gulf of Oman, upwelling allows the development of kelp beds on coral reefs within the tropics.

The answers to the related questions of the source of nutrients to support macroalgal growth, and the time course of macroalgal versus coral domination of benthic communities at the Abrolhos lie in an improved understanding of the regional oceanography, and of the geological growth history of these reefs. The necessary research is in progress (Pearce *et al.* 1991, Collins *et al.* 1991) and the results will provide the best evidence to date on the role of the Leeuwin Current in the development of coral reefs along the coast of Western Australia.

Conclusion

It was obvious to naturalists of the last century that the regional oceanography of Western Australia controlled the development of reefs along its coast (Saville-Kent 1897). We are now in a position to state the obvious with some authority, and to frame testable hypotheses about the mechanisms of control. The definitive statements, however, must await the next century.

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Seabird abundance, distribution and breeding patterns in relation to the Leeuwin Current

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Abstract

Lack of upwelling, and low marine productivity, results in seabirds being much less abundant off Western Australia than along the coasts of western South America and south-west Africa. The breeding and non-breeding distributions of seabirds appear to be influenced by the presence of the Leeuwin Current, as do the timing and success of their breeding activity. For instance, in a year of strong Leeuwin Current flow, Little Penguins near Perth carried less food, were in poorer condition and laid eggs much later than in a year of weaker flow.

Abundance

On the western coasts of southern continents, regions of coastal upwelling often support rich, but locally restricted, seabird assemblages. The diversity of species in these communities is often similar but their abundances may differ greatly. Off Peru, about four million Peruvian Boobies *Sula variegata* breed, together with three million Guanay Cormorants *Phalacrocorax bougainvillii* and one million Peruvian Pelicans *Pelecanus thagus* (Duffy *et al.* 1984). The total numbers of seabirds off Peru are thought to have varied between four million and 20-30 million over the last century (Duffy & Siegfried 1987). Off the south-western coast of Africa the most abundant breeding seabirds are the Cape Cormorant *Phalacrocorax capensis* (280,000), the African Penguin *Spheniscus demersus* (170,000) and the Cape Gannet *Sula capensis* (80,000 birds).

Off the western coastline of Australia, upwelling is much less pronounced than along the coasts of western South America or south-west Africa (Pearce 1991), and populations of seabirds are much smaller (Serventy *et al.* 1971). Indeed, seabird densities off Western Australia were never large enough to accumulate massive guano deposits like those harvested off south-western Africa, Chile and Peru.

In most years, the Benguela and Humboldt Current systems off the western coasts of southern Africa and South America, and the associated upwellings which bring nutrients into the euphotic zone, result in large schools of pilchards, sardines, anchovies and sprats, which provide food for seabirds. It has long been known that seabird populations in the Peruvian and Ecuadorian coastal areas periodically experience major natural disasters due to malnutrition. A warm southward countercurrent usually only displaces the cold, north-flowing water between December - January and March - April, but occasionally strengthens and persists for a year or more, thereby reducing fish stocks (Schreiber & Schreiber 1984).

It is unclear how far the Leeuwin Current affects the abundances of seabirds off south-western Australia but the current has been linked to the changing distributions of seabird species in this region and to their patterns of breeding (Dunlop & Wooller 1990).

Non-breeding distributions

Pelagic seabird species from the Pacific Ocean recently recorded from the waters off Western Australia have been attributed to a marine continuity between the Leeuwin Current and the tropical, western Pacific Ocean (Dunlop *et al.* 1988a). These species include Tahiti Petrels *Pterodroma rostrata*, Bulwer's Petrel *Bulweria bulwerii*, Streaked Shearwaters *Calonectris leucomelas*, Hutton's Shearwaters *Puffinus huttoni*, Fluttering Shearwaters *P. gavia* and Matsudaira's Storm-petrels *Oceanodroma matsudairae* (Dunlop *et al.* 1988a, 1988b).

Breeding distributions

Along the western coast of Australia, some tropical seabirds breed much further southward than in eastern Australia, or even elsewhere in the world (Serventy *et al.* 1971). Common Noddies *Anous stolidus*, Lesser Noddies *A. tenuirostris* and Sooty Terns *Sterna fuscata* all have large breeding populations on the Houtman Abrolhos, well beyond their normal latitudinal limits

(Harrison 1983). Roseate Terns *Sterna dougallii* breed in Warnbro Sound and Bridled Terns *S. anaethetus* off Cape Leeuwin, both reaching the southernmost limits of their worldwide breeding ranges off the Western Australian coast.

Some marked extensions of breeding range have also been recorded relatively recently. After colonising Lancelin Island, probably from Abrolhos populations, the Roseate Tern started breeding in the Fremantle area about 1982 (Dunlop & Wooller 1986). Bridled Terns occurred no further south than the Abrolhos in 1839-1843, reached the Safety Bay islands by 1920, bred on Hamelin Island by 1955 and off Cape Leeuwin by 1957 (Serventy *et al.* 1971). On Penguin Island, in Shoalwater Bay, no Bridled Terns bred in 1940-42 but a substantial, and growing, breeding population had become established by the early 1980s (Dunlop *et al.* 1988c).

The Red-tailed Tropicbird *Phaethon rubricauda* has bred intermittently on the Houtman Abrolhos and from 1957 to 1959 on Rottnest Island (Storr 1964, Serventy *et al.* 1971), although the nearest large, stable breeding population of this species is on Christmas Island, in the eastern Indian Ocean (Harrison 1983). More recently, a small population of Red-tailed Tropicbirds have bred off Cape Naturaliste since 1966 (Serventy *et al.* 1971). The distributions of all these essentially tropical species appear to reflect the influence of the Leeuwin Current.

Seabird assemblages off southwestern Australia are often paradoxical, for instance near Fremantle, where tropical Bridled and Roseate Terns breed beside cool-water Little Penguins *Eudyptula minor*. On the Abrolhos, tropical Sooty Terns, Common Noddies and Lesser Noddies breed on the same islands as cool-water species such as Little Shearwaters *Puffinus assimilis*, White-faced Storm-petrels *Pelagodroma marina* and Pacific Gulls *Larus pacificus*. Off the south-west corner of Australia, Bridled Terns and Red-tailed Tropicbirds nest alongside species from cooler southern waters, such as the Fleshy-footed Shearwater *Puffinus carneipes*. Such paradoxes may be accounted for by the southward extension of tropical seabirds associated with the Leeuwin Current.

Breeding seasons

In south-eastern and southern Australia, seabirds typically breed in spring/summer, whereas in tropical northwestern and northern Australia most breed between March and June. However, on the mid-western and southwestern coasts of Australia, several seabird species breed both in autumn (March-June) and in spring (August-November), some breeding continuously from autumn to spring. Double-breeding or protracted breeding are seen in Crested Terns *Sterna bergii*, Bridled Terns, Roseate Terns, Pied Cormorants *Phalacrocorax varius*, Silver Gulls *Larus novaehollandiae* and Little Penguins (Dunlop & Wooller 1986).

Roseate Terns breed on islands from the Houtman Abrolhos to the Fremantle area in either autumn or spring, the seasonally distinct breeding groups being interspersed throughout these islands. On the Abrolhos, and several other islands, both autumn-breeding and spring-breeding colonies occur on the same island. Of the two recently established colonies, Roseate Terns breed in spring on Lancelin Island but in autumn in Shoalwater Bay (Dunlop & Wooller 1990). Most Crested Terns in southwestern Australia breed from August to December, but autumn-breeding colonies are known from the Houtman Abrolhos, the Fremantle area and east of Hopetoun. On Rottnest Island, autumn breeding did not appear to start until about 1977-1978, presumably as a result of an invasion of autumn-breeders from colonies on the Abrolhos or off the Pilbara coast (Dunlop & Wooller 1990). Detailed observations of individually marked Crested Terns in the Fremantle area have shown that individuals have a broadly circannual reproductive cycle and comprise two groups which are reproductively distinct, although some young born in spring have joined the autumn-breeding group (Dunlop 1985, Dunlop & Wooller 1990).

In the Silver Gull and the Little Penguin, breeding is greatly protracted and egg-laying shows two or more peaks. Both species are potentially double-brooded and readily replace lost clutches (Nicholls 1974, Wooller & Dunlop 1979, Dunlop *et al.* 1988b). Thus, protracted breeding results from sequential, successful, and unsuccessful, breeding attempts by the members of a single population, rather than by separate populations, as seen among terns.

Breeding success

The timing, strength and characteristics of the Leeuwin Current vary seasonally and from year to year. This variability appears to affect the reproductive performance of some seabirds, such as Little Penguins. Since 1986, most of the five hundred Little Penguins breeding on Penguin Island, near Rockingham, have been individually marked, measured and their reproductive success monitored in 55 nest-boxes and a similar number of natural nest-sites in bushes. The stomach contents of penguins coming ashore at dusk in 1986 and 1989 were also analysed (Klomp & Wooller 1988, Wienecke 1989).

In 1989, the mean body weights of male and female Little Penguins were significantly less than during 1986 (Table 1; $t = 13.77$ for males and $t = 7.90$ for females, both $p < 0.01$). These samples did not include moulting penguins but even non-moulting penguins vary seasonally in weight. Therefore, a condition index was calculated (body weight (g) ÷ (head length (mm) + beak depth (mm))) to compare condition independently of size. In 1989, both males and females had significantly lower condition indices than during 1986 (Table 1).

Table 1

The weights and condition of Little Penguins on Penguin Island, Western Australia, and their reproductive performance in 1986 and 1989. Sample sizes are shown in parentheses.

	1986	1989
Leeuwin Current	weaker	stronger
Sea surface temperature	cooler	warmer
Mean (±S.E.) body mass (g)		
Males	1570 ± 19 (152)	1432 ± 16 (145)
Females	1363 ± 13 (143)	1181 ± 13 (132)
Mean (± S.E.) condition index (g)		
Males	125 ± 12 (208)	117 ± 12 (200)
Females	118 ± 10 (182)	106 ± 10 (159)
Mean clutch size	1.9	1.9
Mean (±S.E.) egg weight (g)	53.8 ±0.7	53.8 ±0.2
Mean (±S.E.) egg length (mm)	56.2± 0.5	56.6± 0.3
Mean (±S.E.) egg width (mm)	42.6 ± 0.3	42.3 ±0.3
Percentage eggs hatched	64% (198)	65% (120)
Mean young per pair	0.6 (104)	0.7 (63)

The first penguin eggs were laid in April in both years and laying continued until December, typical of other years monitored. However, the main laying period was 1-2 months later in 1989 than 1986 (Figure 1). In addition, a lower proportion of birds bred in 1989 than in 1986, although clutch size, egg dimensions, hatching success and overall reproductive output were almost identical in both years (Table 1).

Of the 128 penguins sampled in 1989, 15.6% carried no food, significantly more than the 6.3% of 234 penguins sampled in 1986 ($X_1^2 = 72.1$, $p<0.001$). The samples from penguins with food in 1989 (12.5 ± 2.1 g) were much smaller than in 1986 (57.2 ± 10.3 g). However, the prey taken, mostly small, schooling fish, were very similar in both years (Figure 2).

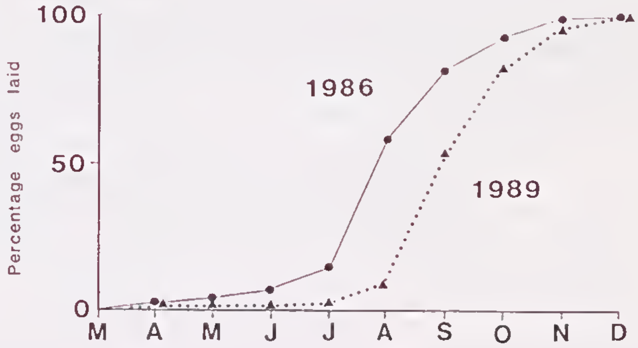

Figure 1 The cumulative monthly percentage of eggs laid by Little Penguins monitored on Penguin Island, Western Australia, during 1986 and 1989.

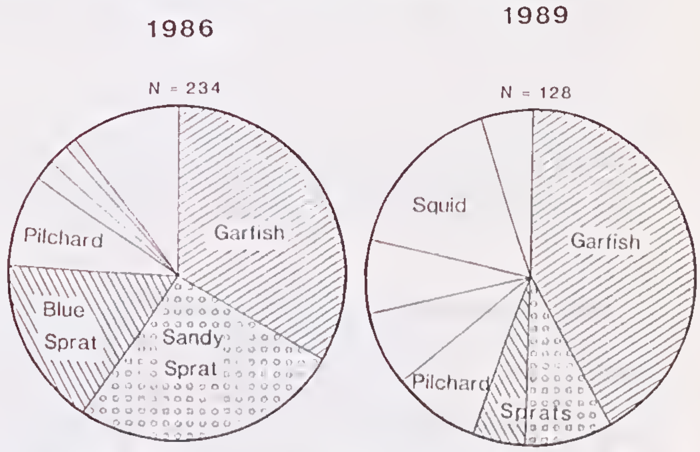

Figure 2 The composition of food samples obtained from Little Penguins ashore on Penguin Island, Western Australia, during 1986 and 1989.

Sea surface temperature at the edge of the continental shelf, near Perth, varied seasonally in a similar manner in both 1986 and 1989, but was up to 2°C warmer in 1989 (Figure 3). Temperatures closer inshore, where penguins feed, paralleled those further offshore, although they were more variable, with seasonal ranges of about 8°C inshore and 5°C offshore. The mean annual sea level at Fremantle, an indicator of the presence and strength of the Leeuwin Current (Pearce & Phillips 1988), was high in 1989, following a similarly high level in 1988. In contrast, 1986 and 1987 had low mean annual sea levels at Fremantle, presumably reflecting a much weaker Leeuwin Current, and cooler surface waters, in those years.

Food samples were not taken from Little Penguins during 1987 and 1988. However, the condition of the penguins was relatively good during 1987 but poorer in 1988. In 1989, the later laying period, poorer condition and lower proportion of birds breeding may have resulted from a warmer sea surface temperature adversely affecting the Little Penguin, which is essentially a cool-water species. This effect is, presumably, mediated through a lower abundance or availability of the schooling fish which form the diet of these penguins. Commercial catches of baitfish were,

indeed, lower in 1989 than in 1986 (R. Lenanton, pers. comm.) but, in the absence of detailed information on fish stocks and distribution, it is only possible to infer the links between oceanographic events and seabird reproductive success at present.

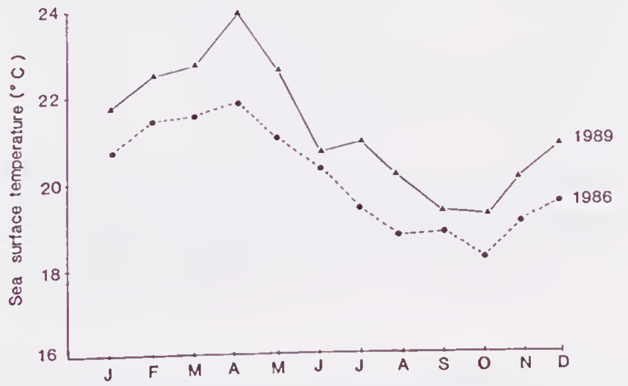

Figure 3 Mean monthly sea surface temperatures (°C) off Rottnest Island, Western Australia, during 1986 and 1989. Data kindly provided by A.F. Pearce.

The invariability in the reproductive effort and success of those penguins which did breed may represent the minimal viable effort in accord with genetic fitness. The non-breeding individuals appear to defer breeding until later in the season, or until a later year, rather than attempt to breed sub-optimally. This strategy may have evolved under the variable oceanographic, and probably trophic, conditions produced by the Leeuwin Current. Interestingly, the Bridled Tern, a tropical species, appears to show a converse effect, arriving and laying earlier in years of stronger current flow and warmer sea surface temperatures (Dunlop & Jenkins, unpubl. obs.).

Conclusions

Variation in the strength of the Leeuwin Current appears to influence the reproduction and mortality of seabirds off Western Australia less dramatically than variation in the El Niño -Southern Oscillation can affect seabirds in the eastern and central Pacific. However, the presence of more tropical, and fewer cool-water, seabird species breeding off southwestern Australia seems clearly linked to this warm water current. The timing and duration of breeding seasons in the region also appear to reflect the seasonal effects of the Leeuwin Current, although much remains to be learned about the mechanisms underlying these relationships.

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Implications of long-term climate change for the Leeuwin Current

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Abstract

The Leeuwin Current is an anomalous, poleward flowing, eastern boundary current, which brings water (and associated marine biota) of warm tropical origin to the temperate south-west and the Great Australian Bight. The Current is driven by an alongshore steric height gradient which is due to the inter-connection between the Indian and Pacific oceans through the Indonesian Archipelago and the density structure of the Indian Ocean.

The Current flows all year round but exhibits a strong seasonality with the stronger flows occurring during the winter months (May - July) and is weaker during the summer (December to January). This is reflected in the coastal sealevels off Western Australia which may be used as an indication of the strength of the current. During ENSO events, the Current is also weaker due to changes in the equatorial Pacific Ocean.

Under an 'Enhanced Greenhouse' warming scenario, there is potential for the driving force of the Leeuwin Current, and its consequent influence on the biota of coastal waters, to be changed. This paper reviews the driving mechanisms of the Current and its annual and inter-annual variability. Selected scenarios under an enhanced greenhouse warming are examined to determine their impact on the strength and location of the Leeuwin Current. It is shown that, although there is a degree of uncertainty on the likely manifestations of the enhanced greenhouse effect, various scenarios indicate a possible decrease in the alongshore steric height gradient resulting in a weaker Leeuwin Current. An increase in the northward wind stress during the summer months is also predicted which could lead to a weaker Current during the summer months than present and more frequent upwelling along the West Australian coast.

Introduction

Increased emissions of carbon dioxide, methane, chlorofluorocarbons (CFC's) and nitrous oxide from human activity have resulted in additional warming of the Earth's surface. This is termed the 'Enhanced Greenhouse Effect' (IPCC 1990). The global mean air temperature is predicted to rise at a rate of 0.3°C per decade (with an uncertainty range of of 0.2°C to 0.5°C per decade) over the next century. Associated with this warming is a re-distribution of heat resulting in changes to the global climate system. This, in turn, will alter the global precipitation patterns, weather systems, frequency of climate extremes and also produce a rise in the mean sealevel (IPCC 1990). The ocean circulation is driven mainly by the global heat budget and, hence, it is envisaged that changes to the global ocean circulation may result from the enhanced greenhouse effect. This paper examines the possible effect of climate change on the strength and location of the Leeuwin Current off Western Australia.

The Leeuwin Current, a poleward eastern boundary current off the West Australian (WA) coast, is a shallow (< 300 m) narrow band (< 100 km wide) of relatively warm, lower salinity water of tropical origin that flows southward, mainly above the continental slope from Exmouth to Cape Leeuwin (Cresswell & Golding 1980, Pearce & Cresswell 1985, Church *et al.* 1989, Cresswell 1991). At Cape Leeuwin it pivots eastward, spreads onto the continental shelf and flows towards the Great Australian Bight. Satellite imagery has shown that the Current is a complex of meanders, jet-like streams and eddies, and the structure and behaviour of the Current vary monthly (Legeckis & Cresswell 1981, Pearce 1985, Prata & Wells 1990, Pattiaratchi *et al.* 1990). The Current is an important feature locally as it influences the climate of Western Australia (Gentilli 1991) and the local fishing industry (Pearce & Phillips 1988, Stequert & Marsoc 1989, Lenanton *et al.* 1991).

Similar to the other southern hemisphere ocean basins, the Indian Ocean accommodates a general anti-clockwise gyre which includes the westward flowing

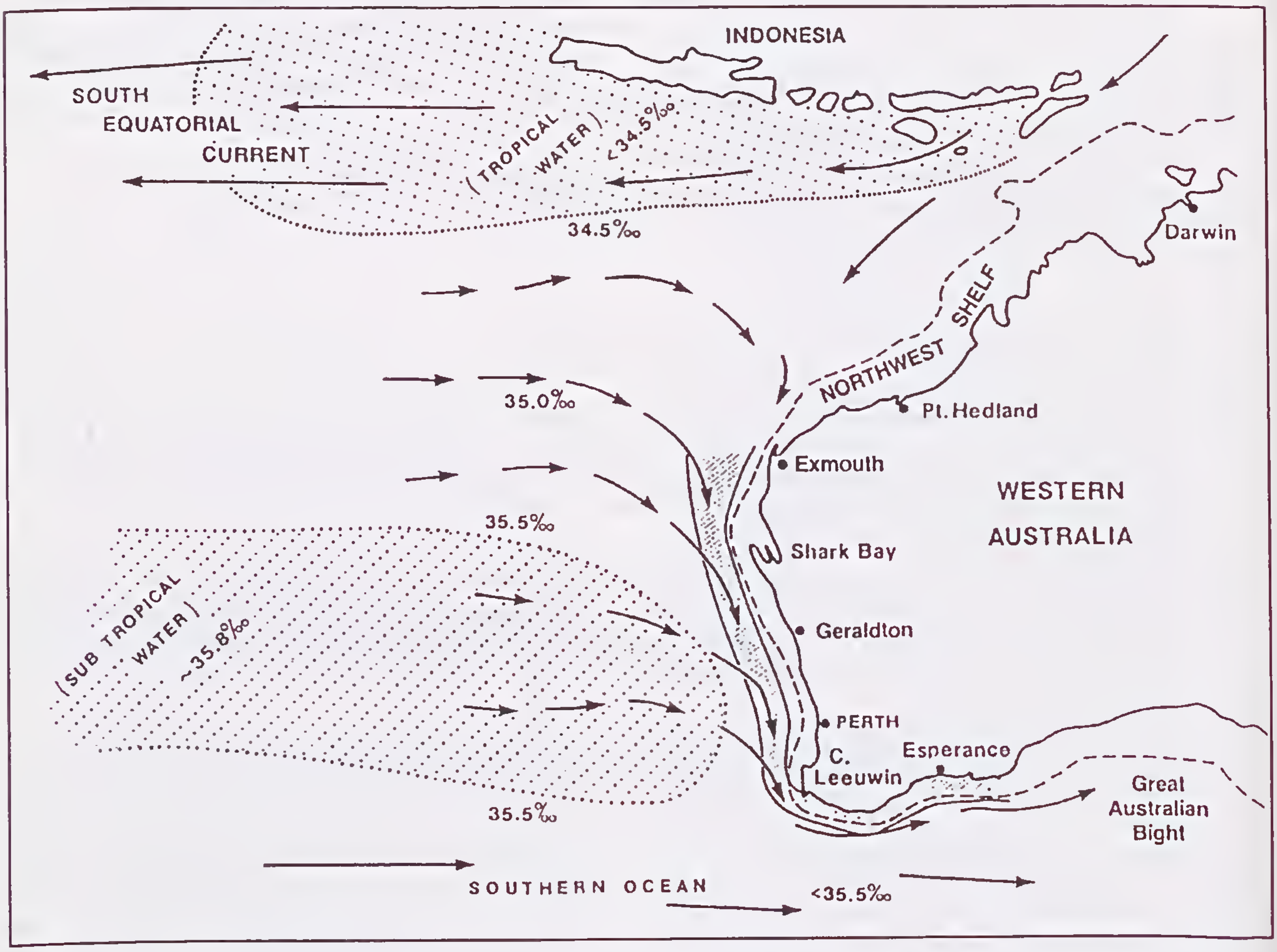

Figure 1 Schematic chart of the large-scale circulation in the eastern Indian Ocean. The Leeuwin Current is shown as the hatched area off Western Australia (From Pearce & Cresswell 1985).

South Equatorial Current from 5°S to 15°S latitude, the strong southward flowing Agulhas Current off the east coast of Africa and the eastward flowing West Wind Drift south of 40°S latitude. Traditional models of ocean circulation postulate a broad, northward return flow off the WA coast, termed the West Australian Current (see for example Tchernia 1980). However, although a net northward flow of water must exist to maintain continuity of the water circulation, field studies undertaken during the 60's and 70's failed to provide any evidence for this equatorward flow. With the advent of satellite tracked drogues and infra-red satellite imagery, the poleward flowing Leeuwin Current was identified (Cresswell 1991). It is now known that the West Australian Current is located seaward of the Leeuwin Current and may extend over more than half of the Indian Ocean as a very slow return flow towards the equator (Thompson & Veronis 1983).

A unique feature of the Indian Ocean circulation is the inflow from the Pacific Ocean through the Indonesian Archipelago. With the exception of the common inter-connection between all the oceans with the Southern Ocean, this is the only connection between any two ocean basins and is an important factor in the generation of the Leeuwin Current.

This paper investigates the possible effect of long-term climate change on the strength and location of the Leeuwin Current by reviewing the proposed generating mechanisms of the Current and the observed variability on seasonal and inter-annual time scales. Various greenhouse scenarios (see for example, IPCC 1990) are examined to identify predictions which may alter the driving forces of the Current. Assuming that any change to the generating forces, as a result of climate change, will influence the strength and location of the Current, predictions are made on the likely behaviour of the Leeuwin Current under an enhanced greenhouse scenario.

Generating mechanisms

Mechanisms for the generation of the Leeuwin Current have been studied by several investigators (Church *et al.* 1989, Godfrey & Ridgway 1985, Pearce & Cresswell 1985, Thompson 1984, 1987, Weaver & Middleton 1989, Batteen & Rutherford 1990, Godfrey & Weaver 1991). There is general consensus that the driving force of the Leeuwin current is an alongshore

steric height gradient which overwhelms the opposing equatorward wind stress. The source of the Leeuwin Current water is from the Indian Ocean from the west and a component (which originates from the Pacific Ocean) from the North West continental shelf. The South East Trade Winds, in the Pacific Ocean, drive the South Equatorial Current westwards advecting warm surface waters towards Indonesia. This results in the flow of warm, low-salinity water from the western Pacific Ocean through the Indonesian Archipelago into tropical regions of the Indian Ocean. This, together with geostrophic inflow of water from the Indian Ocean, results in the sealevel in the tropics being some 55 cm higher than that along the southern coast of Australia (Pearce & Cresswell 1985). The formation and location of the Leeuwin Current are illustrated schematically in Fig. 1.

The meridional gradient of steric height induces a weak geostrophic eastward flow of central Indian Ocean subtropical water toward the coast, between latitudes of 15°S and 35°S. The easterly flow of subtropical water is deflected southward along the edge of the West Australian continental shelf. In the north, the inflow is augmented by tropical water from the North West Shelf. Further south, the continuous inflow from the west accelerates the flow towards Cape Leeuwin, before it turns eastward into the Great Australian Bight. The relative contributions of North West Shelf and central Indian Ocean water, and the mechanism for sustaining the strong meridional steric height gradient, are still under investigation.

Initial investigations (Godfrey & Golding 1981) suggested that the Pacific-Indian Ocean throughflow may be sufficient to sustain the Leeuwin Current. More recent modelling studies (Godfrey & Weaver 1991, Weaver & Middleton 1989) indicate that the Leeuwin Current is largely unaffected by the throughflow magnitude (though the density profile water in the Indonesian region is important, since it controls the longshore pressure gradient along the Leeuwin Current). McCreary *et al.* (1986) suggest that vertical mixing is necessary to support the steric height gradient. The modelling work of Batteen & Rutherford (1990) confirms that the Leeuwin Current can be maintained by the mean thermal structure of the Indian Ocean, but it may be enhanced by the addition of warmer North West Shelf waters. Godfrey & Weaver (1991), using climatological data from Levitus (1982), argue that the propagation of internal Kelvin waves through the Indonesian Archipelago and subsequent western propagation of internal Rossby waves, allows for approximate equilibrium of the specific volume anomaly (SVA) profiles (in the upper few hundred metres) on the North West Shelf, with those in the western equatorial Pacific. The resulting relatively warm pool of surface water, means that surface temperatures are above global equilibrium temperatures (Haney 1971) for west coast water south of 15°S latitude. Consequently, the water of the Leeuwin Current may be expected to lose heat to the atmosphere, resulting in convective overturn and the formation of deep mixing layers. This is confirmed by the observations of Hamilton (1986). There now seems to be general acceptance of the importance of this surface cooling in maintaining the strength of the meridional steric height gradient.

Observed variability

Seasonal changes

In order to examine the fluctuations in the strength of the Leeuwin Current over seasonal and inter-annual time scales, some measure of the intensity of the Current over the complete geographic area of influence is required. In the absence of continuous field measurements of currents, some other measurement related to the Leeuwin Current must be used. Using sea surface temperature (SST) distributions derived from satellite imagery, Prata *et al.* (1989) have defined a 'Leeuwin Current Index (LCI)'. However, the availability of satellite derived SST distributions is limited (approx. 10 years of data) and hence cannot be used to examine long-term changes. Many investigators (see for example, Sturges 1974, Reed & Schumacher 1981, Pearce & Phillips 1988) have shown that changes in mean sealevel monitored at tide gauges may be used to derive oceanographic information such as variations in flow and/or changes in thermohaline properties. For the Leeuwin Current, Pearce & Phillips (1988) have assumed that changes in the strength of the Current are reflected in mean sealevel changes which have an annual mean amplitude of 20 cm (Fig. 2). During October to March the Leeuwin Current is weaker as it flows against the maximum southerly winds, whereas between April and August the Current is stronger as the southerly winds are weaker (Godfrey & Ridgway 1985).

This is reflected in both the SST distributions derived from satellite imagery (Prata *et al.* 1989, Pearce & Prata 1990) and the mean sealevel at Fremantle (Fig. 2).

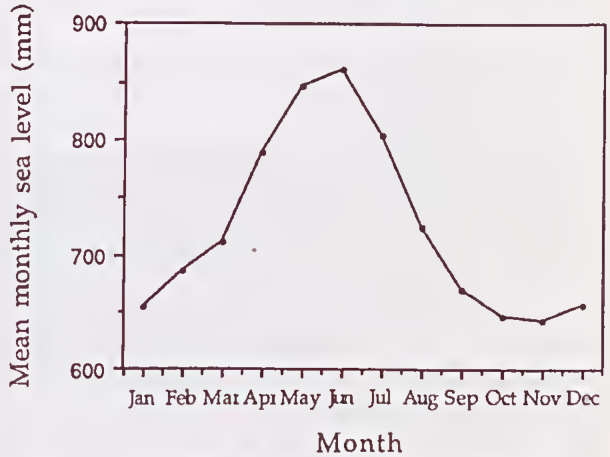

Figure 2 Monthly mean sealevel at Fremantle between 1959 & 1989 indicating that the sealevel has a seasonal amplitude of 20 cm and the maximum occurs during June (Data courtesy of the Tidal Laboratory, Flinders Institute for Atmospheric and Marine Science).

Here, the sealevel is higher between April and August when the Leeuwin Current is stronger (lower wind stress) and lower between October and January when the Current is weaker (high wind stress).

Geographical distribution of the seasonal variations in mean sealevel along the west coast of Australia indicates a progressive feature (Fig. 3 and Pariwono *et al.* 1986). On the North West Shelf, the maximum occurs during March whilst in the South West corner, the maximum occurs in May or June (Fig.s 2 and 3); this seasonal movement of the sealevel maximum reflects the southward passage of the Leeuwin Current pulse (Church *et al.* 1989).

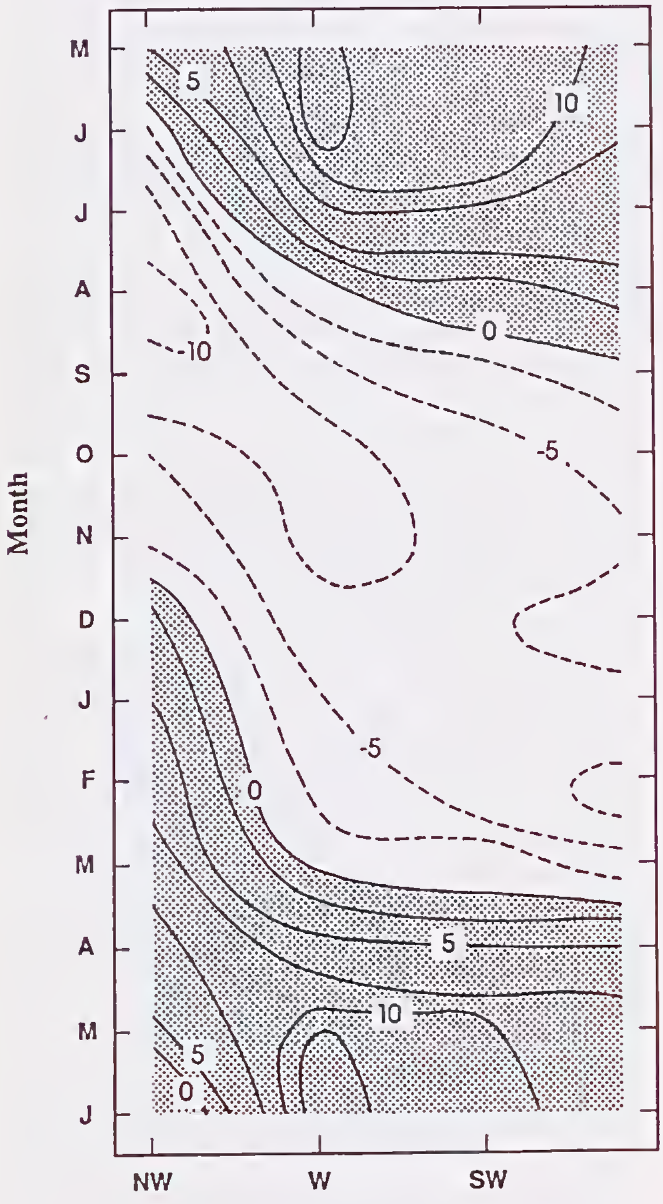

Figure 3 Geographic distribution of the seasonal variation in sealevel (cm) along the Western Australian coastline. Port Groups: NW - north-west (Darwin and Port Hedland); W - West (Geraldton, Fremantle and Bunbury); SW - south-west (Albany and Esperance). (after Pariwono *et al.* 1986).

In summary, although the Leeuwin Current flows all year round, it exhibits a strong seasonality with the stronger flows occurring during the winter months (May - July) which is reflected in the coastal mean sealevel (Fig. 2). Godfrey & Ridgway (1985) have also shown that there is a very good correlation between the coastal mean sealevel at Geraldton and the steric sealevel. Hence, the mean sealevel at Fremantle (or at any other south-west coast station) may be used as an indicator of the strength of the Current.

Inter-annual Changes

El Niño-Southern Oscillation (ENSO) events are the result of complex interactions between the ocean and the atmosphere in the tropical Pacific Ocean and have been associated with climatic and environmental anomalies around the world (Philander 1990). Two or three times each decade anomalously warm water, approximately 2-4°C above normal, appears off the coast of Peru and Ecuador and persists for a number of seasons. Normally the Peruvian coast is a region of strong coastal upwelling (Pearce 1991). During ENSO events, however, warm equatorial water from the western Pacific Ocean is transported eastward and flows southwards along the Peruvian coast to replace the cold, nutrient-enriched waters. It is now known (Philander 1990) that during an ENSO event, there is high surface pressure over the western and low sea surface pressure over the south-eastern tropical Pacific Ocean. This coincides with heavy rainfall, unusually warm surface waters and relaxed Trade Winds in the central and eastern tropical Pacific (Philander 1990).

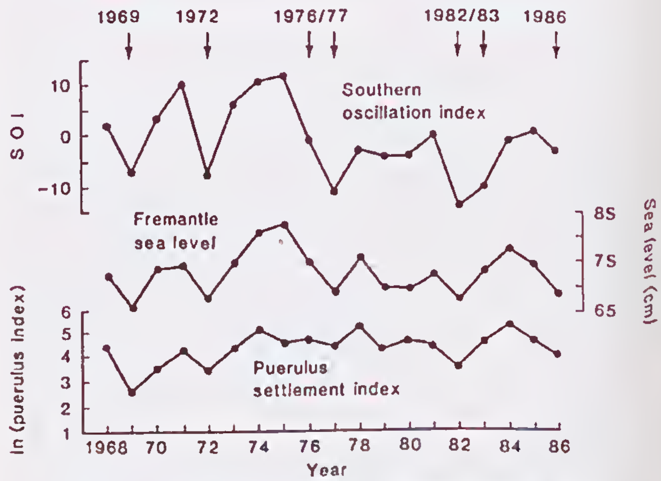

Figure 4 Time series of the annual Southern Oscillation Index (the normalised difference in surface atmospheric pressure between Darwin and Tahiti, a measure of the potential ENSO events), west coast sealevel (a measure of the strength of the Leeuwin Current) and the Puerulus Settlement Index (a measure of rock lobster recruitment) along the West Australian coast (from Pearce & Phillips 1988). The arrows indicate ENSO events.

Pearce & Phillips (1988) have demonstrated a strong correlation between the Southern Oscillation Index (SOI, the normalised difference in surface atmospheric pressure between Darwin and Tahiti, a measure of the potential of ENSO events), west coast sealevels (a measure of the strength of the Leeuwin Current, see above) and the Puerulus Settlement Index (a measure of recruitment to the rock lobster fishery). During normal years, the coastal annual mean sealevels are relatively high indicating that the Leeuwin Current is strong and the settlement of pueruli in coastal reefs is relatively high. During ENSO years, coastal sealevels fall and the inferred transport in the Leeuwin Current is weaker (Fig. 4). Extension of this time series to include the annual Fremantle sealevel data for the period 1897 to 1990 indicates that each ENSO event during this period (extracted from Quinn *et al.* 1987) is associated with a transient decrease in the annual mean sealevel (Fig. 5). This confirms the findings of Pearce & Phillips (1988) and Prata *et al.* (1989) that the Leeuwin Current is weaker during ENSO years.

A weaker Leeuwin Current during an ENSO event may be explained as follows: in a 'normal' situation, the South East Trade Winds in the Pacific Ocean set up high steric heights at the north end of the Australasian continent; the gradient between these high steric heights and the thermally-set low steric height off southwestern Australia drives the Leeuwin Current. During ENSO years, the Trade Winds relax and the steric height at the north end of the Australasian continent is lower. This results in a decreased alongshore pressure gradient along the West Australian coastline resulting in a weaker Leeuwin Current.

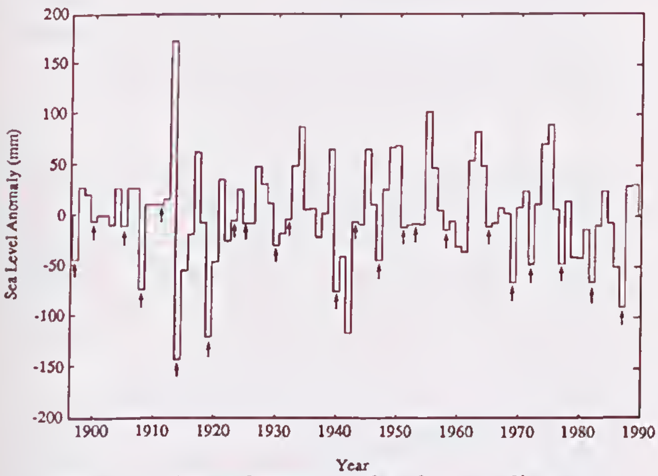

Figure 5 Annual mean sealevel anomalies at Fremantle between 1887 and 1990. The arrows indicate the occurrence of ENSO events as documented by Quinn *et al.* 1987. A decrease in the mean sealevel is seen to be associated with ENSO events (Data courtesy of the Tidal Laboratory, Flinders Institute for Atmospheric and Marine Science).

Scenarios

The dominant issue in the current discussion deals with scenarios for long-term climate change caused by the enhanced greenhouse effect due to increased concentrations of carbon dioxide, methane, CFC's and other trace gases since the industrial revolution. Various scenarios have been proposed based on general circulation model (GCM) simulations (see for example IPCC 1990, Evans 1990) and there is substantial uncertainty on the likely manifestations of the enhanced greenhouse effect. Of these, the following are of relevance in examining the potential changes to the strength and location of the Leeuwin Current.

(i) A global mean air temperature increase of approximately 1°C above the present value by 2025 and 3°C by the end of the next century will lead to a coincident increase in the sea surface temperature. This warming will not be uniform throughout the globe. It is expected that the warming of the mid-latitudes will be higher than in the equatorial regions (IPCC 1990).

(ii) GCM's have so far had limited success in simulating realistic ENSO events (McCreary & Anderson 1991). Hence, there is no clear indication as to the likely changes in the frequency of ENSO events.

(iii) The West Wind Belt (the Roaring 40's) may contract poleward by 5° to 10° latitude, therefore increasing the equator-pole pressure gradients. The Sub-tropical High Pressure Ridge should also move south and may broaden. Weaker Trade Winds are likely (Siegfried *et al.* 1990).

(iv) The mid-troposphere in the tropics will warm to a greater degree than the lower atmosphere, suppressing vertical convection and enhancing wind shear (Evans 1990).

(v) The equatorward alongshore wind stress during the summer months may increase (Bakun 1990).

The different heating rate between the tropics and mid-latitude waters (see (i) above) may result in a decrease in the alongshore steric height gradient driving the Leeuwin Current contributing to a decrease in the strength of the flow.

Weaker Trade Winds in the equatorial Pacific (see (iii) above) may result in a decrease in the strength of the South Equatorial Current (i.e. a decrease in the pooling of warmer water against the Indonesian Archipelago). In terms of the ocean circulation, this effect would be similar to that observed during ENSO events resulting in a weaker Leeuwin Current. The resultant alteration in the specific volume anomaly (SVA) profile in the surface waters would be transferred to the North West Shelf waters, and perhaps lead to a decrease in surface water cooling. This in turn may also reduce the alongshore steric height gradient, weakening the driving mechanism of the Leeuwin Current. Godfrey & Weaver (1991) have shown, from

modelling studies, that if the SVA profile in the western Pacific is replaced by that in the eastern Pacific, a "Peru Current", i.e. equatorward flow together with upwelling, would be established along the West Australian coast. However, current GCM's are unable to predict the likely changes in the SVA profile in the ocean under an enhanced greenhouse scenario and, hence, it is not possible to predict whether a reduced Leeuwin Current or even a "Peru Current" would be present off Western Australia.

Although there is no clear indication as to the likely changes in the frequency of the ENSO events (see (ii) above) a long-term change in the mean value of the Southern Oscillation Index (SOI) would be important for the intensity of the Leeuwin Current. If under an enhanced greenhouse scenario the mean value of SOI increases (decreases), then the Leeuwin Current will be stronger (weaker).

The strong equatorward alongshore wind stress during the summer months is maintained by a strong atmospheric pressure gradient between a thermal low-pressure cell that develops over the heated land mass and the higher barometric pressure over the cooler ocean (Bakun 1990). It has been shown that the Leeuwin Current is weaker during the summer months as it flows against the maximum southerly wind stress (Godfrey & Ridgway 1985). Under an enhanced greenhouse scenario, the gradient between the two pressure systems over land and the ocean may be enhanced, resulting in an intensification of the equatorward wind stress (see (v) above). This would lead to further weakening of the Current during the summer months with the possibility of more frequent upwelling. Analysis of wind data from the major oceanic upwelling areas (Peru, California, Canary Current systems) have shown (Bakun 1990) that the equatorward alongshore wind stress has increased over the past 40 years leading to an intensification of the coastal upwelling systems. This result may indicate that the equatorward wind stress has already increased due to the enhanced greenhouse effect (Bakun 1990).

Implications for Biota

The presence of tropical marine organisms off the west coast of Australia and in the Great Australian Bight has been attributed to the Leeuwin Current (Maxwell & Cresswell 1981, Cresswell 1985). The Current also plays an important role in the life cycle of the southern blue fin tuna (*Thunnus maccoyii*) which has it's spawning area off the North West Shelf (Fig. 6). The larvae and young fish (< 2 years old) are carried southwards by the Leeuwin Current and are found in the Great Australian Bight and off the east coast of Australia. Papers appearing in this issue have also identified the role of the Leeuwin Current in the distribution of seagrass and algae (Walker 1991), coral spawning and distribution (Simpson 1991, Hatcher 1991), western rock lobster (Pearce & Phillips 1988), coastal scallop and fin fish stocks (Lenanton *et al.* 1991) and the sea bird distribution (Wooller *et al.* 1991). Hence, it is clear that the Current plays a major role in the biota off the west and south coasts of Australia

With regard to possible changes in the Leeuwin Current under an enhanced greenhouse scenario, those marine organisms which are dependent on higher temperatures associated with the Current may not be greatly influenced, as a slackening of the Current may be countered by a global sea surface warming. Biota which are dependent on the advective processes of the Current, such as the western rock lobster and southern blue fin tuna, may be more seriously affected. However, a weaker Leeuwin Current and an increase in the northward wind stress may also give rise to more frequent coastal upwelling (see above). This alternate nutrient enrichment may enhance the productivity associated with the continental shelf waters.

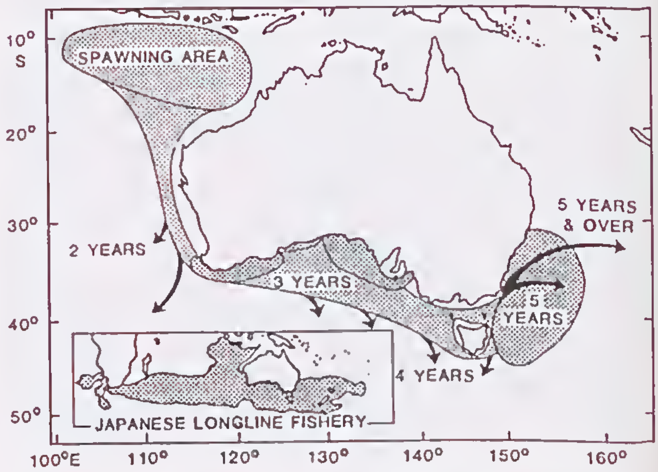

Figure 6 Spawning area and principal migration routes of the Southern blue fin tuna (*Thunnus maccoyii*). The dotted areas show the Australian fleet fishing grounds (from Stequert & Marsac 1989).

Conclusions

This paper has reviewed the proposed generating mechanisms of the Leeuwin Current and observed changes at annual and inter-annual time scales. Possible future changes to the location and strength of the Current and associated biota as a result of the enhanced greenhouse warming have been discussed. Based on these, the main conclusions are:

(a) The Leeuwin Current is driven by an alongshore steric height gradient which is generated due to the inter-connection between the Indian and Pacific Oceans through the Indonesian Archipelago (Godfrey & Ridgway 1985) and the density structure of the Indian Ocean (Batteen & Rutherford 1990).

(b) The Current flows all year round but exhibits a strong seasonality with the stronger flows occurring during the winter months as reflected in the mean sealevel at coastal stations. This annual variation in the Current is due mainly to changes to the northwards component of wind stress and also to a

slight reduction in the steric height gradient. During October to March the Leeuwin Current is weakest as it flows against the strong northwards wind stress, whereas between April and August the Current is strongest as this wind stress is weaker.

(c) The mean sealevel at Fremantle (or at any other south-west coast station) may be used as an indicator of the strength of the Current.

(d) During ENSO events, the Trade Winds relax and the South Equatorial Current in the equatorial Pacific is weaker with a corresponding decrease in the alongshore pressure gradient resulting in a weaker Leeuwin Current.

(e) Although there is great uncertainty on the likely manifestations of the enhanced greenhouse effect, various scenarios relevant to determining the strength and location of the Current indicate a possible decrease in alongshore steric height gradient which may result in a weaker Leeuwin Current.

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